SOCIAL INFLUENCES ON VISUAL ATTENTION IN PRIMATES

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DECLARATION

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

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ABSTRACT

Studies of visual attention in primates have generally focused on anti-predatory functions of vigilance, and likewise, social attention is commonly associated with protecting against threat. However, little research has tested whether threat protection provides the best representation of social visual attention in primate groups. Moreover, social monitoring has rarely been considered as a function of social relationships and whether affiliation is important.

This thesis is comprised of a series of studies examining social monitoring in captive chimpanzees, orang-utans and siamangs; and in free-ranging chacma baboons and ring-tailed lemurs. Particular emphasis is placed on considering social monitoring as a dyadic social interaction, involving both an initiator and recipient of attention. This 'social' approach to social monitoring uses dyadic social relationships within the group and attributes of the initiator and recipient to interpret visual attention.

The effects of dyadic relationship quality on visual social monitoring were examined in all the study species. Indices of the strength of affiliative relationships were used to provide a quantitative measure of social relationships and categorise dyads as friends or non-friends. In contrast to standard interpretations of social monitoring, affiliative relationships have a significant influence on the distribution of social monitoring in some primate groups.

Social referencing, a complementary aspect of visual social attention, was also explored in orang-utans using visual responses to naturally

occurring events and orang-utan playback vocalisations. Using this novel approach, this is the first study that documents social referencing in adult orang-utans and that biological relevance and ambiguity are important for seeking reference from conspecifics.

The final section of this thesis considers the visual budgets of the study species, a multi-faceted basis of vigilance in primates, and asks whether the frequency of social monitoring in primate groups can be predicted from a number of variables. Interactive effects of species, context, attention types and targets revealed the complex nature of visual attention in primate groups. Social variables contributed strongly to the variability in primate social monitoring.

The findings indicate that visual attention reflects social relationships in primate groups. The predominantly affiliative nature of primate social interactions suggests the influence of threat protection on social attention has been overemphasised. Accordingly, visual social attention plays an important role in social interactions, permitting individuals to monitor group dynamics, seek information and respond to changes appropriately.

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CHAPTER 1

THE SOCIAL NATURE OF PRIMATE VISUAL ATTENTION

Overview

In this thesis, I focus primarily on one component of social visual behaviour known as social monitoring, which is typically considered within the broader context of vigilance behaviours. Beyond the raw frequency of social monitoring occurring within a group, little is known about its significance for primates. We need to know who monitors whom, how often and when. There is also some concern that most studies accept the default explanation of social monitoring - namely protecting against threat, without critically evaluating its assumptions or testing alternative hypotheses.

In the first part of this introductory chapter, I take a critical look at what is known about social influences on visual attention in primates. The second half of this chapter introduces a 'social' approach to social monitoring which considers monitoring of conspecifics as a dyadic interaction and argues that social monitoring may be indicative of the relationship between individuals. Additional factors thought to influence social monitoring such as season, competition, context and proximity are also discussed. Assessing the dyadic relationship between individuals using multiple social variables, may help explain why primates spend considerable time visually attending to conspecifics. Using this perspective, we might gain a better understanding of the proximate mechanisms that enable primates to live together and maintain their social relationships.

The importance of visual communication for primates

Diurnal primates rely heavily on visual monitoring behaviour to collect various kinds of ecological and social information. The primate brain contains 32 areas that are exclusively dedicated to visual processing (Felleman & van Essen, 1991) with specific regions and neurons adapted to the processing of socially relevant signals (Treves & Pizzagalli, 2002).

Traditional ethological studies of primate behaviour have long recognised the important role that the eyes play in communication (reviewed in Emery, 2000; van Hooff, 1967). Direct eye gaze may serve an aggressive function in many primates; however, primates in a close relationship also visually attend to one another (Argyle & Cook, 1976; Mitchell, 1972).

Most research of visual social attention in primates has taken place in the laboratory, with particular emphasis placed on the cognitive abilities underlying visual behaviours such as gaze following, using visual cues to locate hidden entities, and visual perspective taking. For instance, many species of primates are able to use another's line of sight to direct their own attention (e.g. Shepherd & Platt, 2008; Tomasello, Call & Hare, 1998). Primates are also adept at using visual cues such as head orientation and body posture to locate a hidden entity, (see Itakura, 2004 for a review) and can predict an individual's behaviour based on their attention (Hare, Call, Agnetta & Tomasello, 2000).

However, less information is available about the factors that influence an individual's propensity to visually attend to another individual. Visual behaviours such as gaze following can only occur if an individual first attends to another. Only once attention to a conspecific occurs, can the conspecific's

gaze be followed. While the ability to use eye gaze within a mentalistic framework is important, I take an ethological approach to visual attention, exploring social variables that influence the frequency and patterning of visual attention. The question of why social monitoring occurs, and why it might be important, firstly requires consideration of general visual attention in primates. The study of vigilance behaviours can help address this question.

Social monitoring and its relation with vigilance

Vigilance is simply defined as looking up from an activity, or as an immediate visual search of the environment beyond the immediate vicinity (Treves & Pizzagalli, 2002). The change in head and/or eye orientation is key when measuring vigilance, as head and pupil orientation is thought to serve as a 'pointer' of attention (Treves, 1998a). Within this perspective, social (e.g. conspecifics), and non-social targets of vigilance (e.g. predators, or environmental features) can usually be revealed by the direction of head and/or eye orientation.

However, vigilance is costly because it involves both time and visual attention (Treves, 2000). Vigilance also conflicts with other activities such as feeding and grooming (discussed in a later section). Therefore if vigilance is costly, what do primates gain from frequent visual monitoring of the immediate environment?

There are four major hypotheses that address reasons why primates are vigilant. The primary explanation is that vigilance is used to detect predators (e.g. Bednekoff & Lima, 1998; Biben, Symmes & Bernhards, 1989; Lima, 1990; Pulliam, 1973; Treves, 2000). Vigilant individuals are able to

respond more quickly to danger (Lima, 1994) and there is some evidence that predators attack less vigilant individuals (Fitzgibbon, 1989). A second explanation specifically addressing vigilance by adult males is related to mate guarding and protection of paternity. While males may be the first to detect predators, it may be a by-product of their motivation to be vigilant towards male competitors who belong to other groups (Baldellou & Henzi, 1992; Gould, Fedigan & Rose, 1997; Rose & Fedigan, 1995). A third explanation for vigilance behaviour is that animals of both sexes may be vigilant in order to protect their resources and their home ranges or territories from intrusion or competition by members of other groups (Baldellou & Henzi, 1992; Rose & Fedigan, 1995; Steenbeek, Piek, van Buul & van Hooff, 1999). This resource defence explanation suggests that most vigilance is directed to conspecifics of other groups rather than predators.

The final explanation for vigilance focuses on the fact that individuals are vigilant towards members of their own social group. Within-group vigilance may serve multiple purposes such as detecting predators through the behaviour of conspecifics, social learning, and monitoring the level of threat and competition within the group (reviewed in Treves, 2000). However, within-group vigilance (hereby referred to as social monitoring), has only recently received detailed consideration, in part, due to the theoretical pre-eminence of predation (Treves, 2000). Studies of vigilance have often excluded visual attention towards conspecifics of the same group because they were explicitly measuring anti-predator vigilance (Baldellou & Henzi, 1992; Gould, 1996a; Hardie & Buchanan-Smith, 1997).

Why do studies of vigilance need to include social monitoring?

Vigilance may serve multiple functions: to spot predators, monitor associates and survey escape routes (Treves, 2000). Therefore the targets of vigilance can generate differences in overall time spent vigilant. Visual monitoring of conspecifics, can also affect predator detection, as conspecifics can reveal they have detected predators through escape or alert postures (Lima, 1994). Even if individuals do not personally locate a predator, they are more likely to flee if they see conspecifics fleeing (Coss & Ramakrishnan, 2000). In short, estimates of vigilance or visual attention are likely to be inaccurate if social monitoring is excluded from the definition of vigilance.

More importantly, social monitoring is also a frequent behaviour (Treves, 2000). Although external risks such as predators and extra-group conspecifics are undoubtedly important, the frequency of interaction with conspecifics within the social group far outweighs the frequency of encountering predators or other troops. Therefore one would expect visual attention to be expended on these frequent social interactions. Social monitoring is not a new phenomenon, yet beyond the raw frequency of this behaviour, inconsistent evidence exists on why conspecifics within the group monitor one another, and what purpose this behaviour serves. This may be due in part to how social monitoring is defined, and the environment in which the data are collected. What is clear, however, is that frequent, time consuming and sensitive attention towards conspecifics is likely to reflect the importance and priority of gathering socially relevant information for primates (Treves & Pizzagalli, 2002).

Defining social monitoring

Vigilance is simply defined by head movement or head re-orientation and social monitoring is usually defined using the same criteria, with the movement of the head and/or eyes directed towards a social target in the group. Commonly, data on social monitoring are collected on individually recognised individuals, towards any conspecific in the group regardless of identity. In some studies of social monitoring in free-ranging primates, individual recognition of focal individuals is sacrificed in favour of sampling multiple groups (Treves, 1999; Treves & Baguma, 2002). While data are collected on attention specifically to social targets, information is lacking on the identity of the conspecifics being monitored (Jack, 2001; Treves, 1999; Treves & Baguma, 2002). Finally, data may be collected on all vigilance, with no differentiation between social and non-social targets of attention. Social behavioural correlates of vigilance are used to infer a social monitoring function of vigilance. For instance, if vigilance increases with a greater number of neighbours, a social monitoring explanation of vigilance (rather than an anti-predatory explanation) is deduced (Alberts, 1994; Chalmeau, Cezilly & Desportes, 1998; Hirsch, 2002; Kutsukake, 2006; 2007).

In order to document social monitoring and why it occurs, it is imperative that the target of social monitoring is identified so that attributes of the initiator and recipient of monitoring are considered together.

Why is social monitoring important?

Primates spend considerable amounts of time watching one another and yet little is known about why social monitoring is significant and the variables

influencing the propensity to monitor conspecifics in the same group. Social monitoring may be used to keep track of friends and allies within the group (Dunbar, 1983; 1988); avoid aggression or dominant animals (e.g. Chance, 1967); maintain coordination and cohesion during travel (Dunbar, 1983; Meunier, Deneubourg & Petit, 2008); regulate inter-individual distance (Rowell & Olson, 1983); trigger sexual arousal (Linnankoski, Grönroos & Pertovaara, 1993) and play a role in mating strategies (Keverne, Leonard, Scruton & Young, 1978).

Social monitoring may also be important for observational learning (Coussi-Korbel & Fragazy, 1995) especially for younger individuals (Querouil & Blois-Heulin, 1998). Visual reference to conspecifics can be used to appraise ambiguous situations, where attention is directed towards another individual to gauge how to react appropriately. This phenomenon, known as social referencing, is well documented in human children (e.g. Baldwin and Moses, 1996) and in young apes (e.g. Russell, Bard & Adamson, 1997).

Given these possible functions and benefits of social monitoring, generally research has only focused on one possible role of social monitoring in primate groups - protecting against threat. An early theory proposed by Chance (1967) and further expanded by Chance and Jolly (1970) proposed simply that social monitoring is a function of rank order in primates and used to avoid aggression.

The social structure of attention

Chance's theory

Chance (1967) proposed that visual social attention in primates served to

maintain group cohesion and social relationships with emphasis on rank ordered social relationships. The central concept of this theory posits that dominant individuals are the focus of attention of those holding subordinate status within the group. Thus, persistent attention by subordinates towards the alpha individual would be enhanced more if the alpha were aggressive. According to Chance (1967), aggression ties attention exclusively to a given individual and consequently visual attention maintains the social relationship and coheres the group.

Chance and Jolly (1970) further expanded the attention structure theory to account for the variability of social organisation and environmental constraints in a number of primate species. Persistent attention to dominant individuals is considered particular to species that form a male defence front towards predators (centripetal societies). Alternatively, social monitoring of dominant individuals is considered less important for species that use concealment or escape from predators (acentric societies). Within a group, why would dominant individuals (particularly the alpha animal) be the focus of attention given the presence of numerous conspecifics to visually attend to? Chance and Jolly (1970) attributed constant attention to dominant individuals as a function of attention getting displays, the frequency of aggression and the maintenance and regulation of distance from dominant animals.

Despite Chance's claims for a rank based attention structure, critics question how attention related to aggressive behaviour could cohere a group. If females and other animals approach an aggressive animal, they must be attracted to it in another way (Hinde, 1974). However, Chance's

theory raises some useful ideas about the structure of attention within primate groups which have subsequently formed the basis of newer studies: specifically, that attention is not distributed equally to all individuals within a group and is influenced by factors such as social organisation, species and by vigilance directed outside the group. The attention structure theory was formulated without quantitative data to support the theory and some early studies provided qualitative information on social monitoring and extended hypotheses rather than testing the original theory.

Table 1.1 summarises primate social monitoring studies that specifically tested for rank and agonistic influences on visual attention to conspecifics. All the studies listed, bar one, feature captive animals and in the majority of studies, groups consist of less than eight individuals. It is clear that agonistic and rank influences on social monitoring are by no means consistent across studies and within species. Data from prosimians and apes are notably absent from this table.

The most commonly used method to test rank and agonistic effects on social visual attention is to correlate the overall frequency of social monitoring (summed across all conspecifics in the group) with the relative rank position of an individual, or with the frequency of aggression received (from all conspecifics in the group).

The next section reviews the evidence for a threat protection function of social monitoring identified by the studies listed in Table 1.1. Alternative motivations for social monitoring such as keeping track of friends are explored further.

Table 1.1 Primate studies that tested for a relation between social monitoring and agonism and/or rank status.

Species	Relation between social monitoring and rank? Given	Received	α receives most attention?	Social monitoring and agonism?	Notes	Source
Squirrel monkey	-	-	-	No		1
Squirrel monkey	S	-	-	-	Food context only	2
Squirrel monkey	No relation	No relation	No	-		3
Capuchin monkey	S	D	No	-		3
Capuchin monkey	S	D	-	Subordinates only		4
Patas monkey females	S	D	-	-		5
Talapoin monkey	S	D	-	Yes	Single sex group	6
Talapoin monkey	No relation	D	-	Yes	Mixed sex group	6
Diana monkey	No relation	No relation	No	-		3
Vervet monkey	No relation	No relation	No	-		3
Red-capped mangabey	-	No relation	No	-	Non preferred food	7
Red-capped mangabey	-	-	Yes	-	Preferred food	7,8
Grey-cheeked mangabey	-	-	Yes	-	Preferred food	8
Long-tailed macaque	S	D	No	-		9
Long-tailed macaque	No relation	D	-	-		10
Rhesus macaque males	No relation	No relation	-	-		11
Mandrill	-	-	Yes	-		12
Gelada baboon	-	-	Yes	-		12
Gelada baboon	No relation	No relation	Yes	-	Free-ranging	13

S denotes subordinates monitor more than dominants; D denotes dominants were monitored more than subordinates; - denotes not tested.

References: 1 Strayer & Gariepy (1986); 2 Caine & Marra (1988); 3 Torres de Assumpção & Deag (1979); 4 Pannozzo, Phillips, Haas & Mintz (2007); 5 McNelis & Boatright-Horowitz (1998); 6 Keverne et al. (1978); 7 Blois-Heulin & Girona (1999); 8 Blois-Heulin & Martinez-Cruz (2005); 9 Emory & Harris (1981a); 10 Pitcairn (1976); 11 Haude, Graber and Farres (1976); 12 Emory (1976ab); 13 Dunbar (1983).

Social monitoring as threat protection

Social monitoring and rank status

Some support for the attention structure theory has been provided by a number of primate species. Studies listed in Table 1.1 suggest that subordinates engage in the highest frequencies of social monitoring, while dominants receive the most monitoring (Caine & Marra, 1988; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998; Pannozzo et al., 2007; Pitcairn, 1976). However, within the group, it is unclear which conspecifics are being monitored.

In uni-male groups, the adult male receives the most attention (Dunbar, 1983; Emory, 1976ab). However, attention towards the alpha animal may occur only when competition exists (Blois-Heulin & Girona, 1999). While Emory (1976b) has reported frequent social monitoring of the alpha male in both mandrills and gelada baboons, data were not provided on the frequency of monitoring of other conspecifics as a comparison. When social targets of attention are examined in more detail, there is less support for the attention structure theory.

For instance, even though the alpha animal may receive the most attention overall (Emory & Harris, 1981a), it is not necessarily the highest proportion of every animal's attention. Middle to low ranking macaques do not focus attention solely on the alpha animal (Emory & Harris, 1981a), and attention is also directed towards salient partners (Dunbar, 1983; Emory, 1976b). In some primate groups, there is little evidence for a rank based attention structure (Dunbar, 1983; Strayer & Gariepy, 1986; Torres de Assumpção & Deag, 1979).

Studies of inferred social monitoring in free-ranging primates also report a varying influence of dominance rank on vigilance. Low ranking individuals are more vigilant than high ranking individuals (Chalmeau et al., 1998; Yamamoto, 2005). Alberts (1994) reported that daughters of low ranking mothers glanced more frequently than daughters of high ranking mothers, while the opposite was true for sons. However, in other studies, there is little influence of rank on vigilance (Altmann, 1980; Hirsch, 2002; Kutsukake, 2006; Rowell & Olson, 1983).

Monitoring aggressors

In three out of the four studies that tested for aggressive influences on social monitoring (Table 1.1), individuals that received high rates of aggression monitored conspecifics at high rates. These findings are problematic because individuals that receive the highest levels of social monitoring are not necessarily the most aggressive (Keverne et al., 1978). It is also unclear within a dyad if A receives aggression from B, whether A monitors more frequently than B. It may be the case that aggressive individuals that attack other conspecifics in the group invoke heightened social monitoring, even if an individual has not been attacked by the aggressive individual (Keverne et al., 1978; Pannozzo et al., 2007). However, data from female gorillas suggest that monitoring may be specifically directed towards female adversaries rather than allies (Watts, 1998).

Monitoring competitors

Social monitoring may be responsive to conspecific competition. When

feeding competition is heightened, i.e. with preferred food or when food distribution is clumped, the frequency of social monitoring may be higher and directed towards higher ranking individuals (Blois-Heulin & Girona, 1999; Blois-Heulin & Martinez-Cruz, 2005).

Treves and Baguma (2002) have suggested that female-female competition is manifested through increased social monitoring in despotic compared to egalitarian species. In multi-male primate groups, social monitoring may be frequent due to more male rivals within the group compared to uni-male groups (Treves, 1999). In capuchin monkeys, male emigration results in decreased social monitoring which is associated with the corresponding decrease in male-male competition (Jack, 2001). During mating season, rates of social monitoring increase significantly (Treves, 1999), but it is unclear whether this monitoring is responsive to male-male mating competition and/or presence of estrous females.

The relation between competition and social monitoring is likely to be linked to group size. Specifically, as group size increases, the balance of vigilance (rather than the total amount of vigilance) is hypothesised to shift from predominantly anti-predator scanning to the surveillance of group mates, as social competition increases within larger groups (Treves, 1999). There is weak support for the group size component of this hypothesis (Treves, 1999). However, some support exists for balancing social and non-social monitoring as a function of the level of competition within a group rather than group size per se (Caine & Marra, 1988, Jack, 2001; Treves, 1999; Treves & Baguma, 2002).

Alternative explanations for social monitoring

Threat protection is generally the accepted explanation of social monitoring. However, affiliation may have an important influence on social monitoring. In pre-school aged children, visual social attention is positively correlated with affiliation (La Freniere & Charlesworth, 1983; Strayer, 1992; Vaughn & Waters, 1981) and negatively correlated with aggression (Vaughn & Waters, 1981). In primates, conspecifics also visually attend to each other when a close relationship exists e.g. mothers and infants, mating pairs, or members of male groups (Argyle & Cook, 1976). Virgo and Waterhouse (1969) and Waterhouse and Waterhouse (1976) have reported high rates of social monitoring towards preferred grooming partners in addition to aggressive individuals (see Emory, 1976b for similar trends concerning play partners). Similarly, gelada females monitor both the unit male and female allies (Dunbar, 1983).

Strayer and Gariepy (1986) compared affiliative and competitive influences on social attention, finding affiliation had a greater influence on attention than competitive and dispersive activities. Indeed the strength of the affiliative bond reflects durations of social monitoring in some primates (Phillips & Mason, 1976).

Social monitoring: previous research and unanswered questions

While some support exists for the attention structure theory, the results are by no means consistent across studies or species. Approximately, half the studies listed in Table 1.1 indicate a relation between rank status and social monitoring. This approach does not answer why a subordinate monitors

frequently or whom the attention of this subordinate is directed towards. If attention is directed to a dominant individual, then the underlying basis of attention still needs to be explored in order to reveal why this dominant animal is frequently monitored be it aggression or another mechanism e.g. a preferred grooming partner (Virgo & Waterhouse, 1969).

Dunbar (1988) has suggested that social monitoring may reflect two motivational states. An individual may monitor conspecifics because it is nervous and/or to keep track of friends. Strayer and Gariepy's (1986) study suggests that affiliation influences who is monitored, and that salient individuals in the group such as allies or play partners may be monitored frequently (Dunbar, 1983; Emory, 1976b). When dyads (rather than individuals) have been considered, it is clear that rank influences on monitoring do not exist for all dyads (Emory & Harris, 1981a) and dyads closer in rank positions may monitor more frequently than dyads with a greater rank difference (Haude et al., 1976).

The attention structure theory suggests that attention is not distributed equally among group members, yet this premise has not been pursued further. If social monitoring reflects two different motivations, it is imperative to consider social monitoring between pairs of animals with reference to their relationship in order to elucidate why some conspecifics are monitored more than others and why social monitoring is important. Without dyadic assessment of attention (i.e. A's attention to B, and B's attention to A) particularly with reference to the relationship between individuals, attempts at understanding the motivations for social monitoring are severely limited by the reliance of rank status as the ultimate cause of social attention.

Accordingly, the emphasis of rank order on social monitoring precludes interpretation of social attention in species with no rank hierarchy.

If Dunbar's (1988) postulation is correct: that social monitoring may reflect two motivational states - nervousness and keeping track of friends - then social monitoring studies to date have only tapped into one aspect of social attention. Few researchers have tested their assumptions that rank position provides the best representation or explanation of social attention structure.

A 'social' approach to social monitoring

In this thesis, I aim to examine the 'social' basis for social monitoring in five species of primates. The emphasis is on the influence of relationship quality between dyads, in that previous studies of social monitoring have neglected the influence of relationship quality, focusing solely on rank status or aggression received. This individual based approach to social attention informs little about who is being monitored and why. Instead, assessing whether relationship quality is affiliative or agonistic may provide a better explanation of the variability of social attention in primate groups and permit assessment of the basis for social monitoring in groups where rank order is weak, unstable or absent. This social approach involves two main components: a) considering social monitoring as a dyadic interaction involving both an initiator and a recipient of attention and, b) using knowledge of social relationships to interpret patterns of social monitoring. This way, the dyadic relationship quality between individuals can be matched up with the visual data and several hypotheses about the basis of monitoring

can be tested. Assessing the influence of relationship quality on social monitoring may help explain why primates spend considerable time visually attending to conspecifics.

Considering social monitoring as a dyadic interaction

Little research explicitly considers the dyadic nature of attention. When assessing rank based attention structure, targets and recipients of monitoring are usually classified as high- or low-ranking, without reference to the nature of the relationship, e.g. frequent grooming partners, kin dyad etc. Accordingly, when considering dyads, the amount of attention given to a partner varies according to the relationship (McNelis & Boatright-Horowitz, 1998; Watts, 1998). Strayer and Gariepy (1986) found symmetry of attention within dyads, which strengthened their argument for a non-competitive interpretation of social attention.

The focus on the individual as the unit of analysis may be related to reliance on statistical techniques such as the analysis of variance, as dyadic data typically violate statistical assumptions (Kenny, Kashy & Cook, 2006). However, dyads have been used as units of analysis in numerous studies of primate social behaviour (e.g. Overdorff, 1998; Silk, Seyfarth & Cheney, 1999; Watts, 2002) using matrix correlational analyses (de Vries, Netto & Hanegraaf, 1993; Hemelrijk, 1990). Dyadic analysis would be revealing for social monitoring as this type of analysis considers the contribution of both individuals towards each other. Additionally, behavioural phenomena involve two individuals, yet these inter-relational concepts are typically measured by examining both individuals in isolation (Kenny et al., 2006). The argument for

a particular attention structure would thus be strengthened if the contribution of one animal was shown to be different from that of its partner.

How relationship quality may influence social monitoring

Why would it be important to monitor affiliates?

Just as monitoring aggressive individuals may be important for avoidance of aggression, monitoring affiliates may be important for maintaining the social bond (Phillips & Mason, 1976) or initiating play (Emory, 1976b). Friendships are maintained by frequent association and behaviours such as grooming (Cords, 1997; Silk, 2002). Subsequently, maintenance of proximity requires visual time and attention (Rowell & Olson, 1983). Distress at losing visual contact with friends has been reported in female chimpanzees (Boesch & Boesch-Achermann, 2000).

Chivers (1974) has suggested that the synchronisation and cohesiveness of siamangs is maintained by frequent monitoring of the group. Similarly, in female gorillas, once visual contact has been established, females tend to follow the silverback male, presumably to maintain proximity (Watts, 1998). Additionally, the formation of alliances would appear to require efficient monitoring of supportive individuals (Dunbar, 1983; 1988; Kutsukake, 2006). Individuals with strong bonds usually form alliance and coalition partnerships (de Waal, 1982; Watts, 2002), thus monitoring may be linked to keeping track of these valuable allies and efforts to remain close.

Recent reviews have questioned the significance of competition and aggression on primate sociality. Sussman and colleagues (Sussman, Andrianasolondraibe, Soma & Ichino, 2003; Sussman, Garber & Cheverud,

2005) argue that social interactions in primates are predominantly affiliative and form the basis for social bonds. If an individual's survival is enhanced by the collective advantages of living in a cohesive, socially integrated behavioural unit, then an understanding of an individual's ability to maintain affiliative behaviours and to minimise agonistic interactions is likely to provide critical insights into the evolution of sociality in primates (Sussman et al., 2005). This argument calls for a more detailed analysis of social attention, as attention may be an important component of primate social behaviour. It is likely that primates possess an adaptive strategy of visually securing the most socially relevant information which may vary from one individual to another and between species.

Why would it be important to monitor aggressors?

Competitive and aggressive threats generated by conspecifics may favour vigilance (Treves & Pizzagalli, 2002) as actions of associates have fitness consequences (Treves, 2000). If social monitoring indexes nervousness (Dunbar, 1988; Mitchell, 1972), then one may expect that individuals that receive frequent aggression also monitor most frequently; and some studies listed in Table 1.1 suggest this is the case. However, there are little data available on whether individuals actually monitor their aggressors. Female gorillas monitor those with whom they possess a poor relationship, but in most cases, the relationship is neutral rather than highly agonistic (Watts, 1998). It may be the case that unresolved dominance and bi-directional aggression (i.e. ambiguous relationships) contribute to increased social monitoring in non-friendly gorillas dyads. While social monitoring is

suggested to be a mechanism of avoiding conflict (Pannozzo et al., 2007), there is little evidence that suggests the most socially vigilant individuals receive the lowest rates of aggression or are able to avoid conflict through heightened social monitoring. Instead, if social monitoring functions to avoid proximity to aggressive animals (Chance & Jolly, 1970), then documentation of patterns of proximity and monitoring of both affiliates and adversaries would help elucidate why receivers of aggression monitor more frequently and if aggressors are avoided.

Assessing competitive influences on social monitoring

Competition during feeding context

A primary cost of sociality in primates is assumed to be increased competition during feeding (Sterck, Watts & van Schaik, 1997; van Schaik 1983; 1989; Wittig & Boesch, 2003). Therefore, consideration of social monitoring during feeding might provide a good estimate of the effect of competition on social monitoring. However, numerous studies have reported reduced vigilance in primates during attentionally demanding activities, particularly feeding (Hill & Cowlishaw, 2002; Hirsch, 2002; Kutsukake, 2006; Treves, 2000; Treves, Drescher & Ingrisano, 2001; Uhde & Sommer, 2002; van Schaik & van Noordwijk, 1989). This is because most animals lower their heads to feed, thereby occluding their visual fields (Treves, 2000). However, research focusing exclusively on social monitoring in captive groups, has reported higher rates of monitoring conspecifics during feeding; this may be related to competition.

Instead of reduced attentiveness during feeding, Blois-Heulin and

Girona (1999); Blois-Heulin and Martinez-Cruz (2005) reported attenuated social monitoring in the presence of preferred food. Social competition may facilitate more social monitoring during feeding in despotic female primates (Treves & Baguma, 2002). However, the influence of competition is not clear-cut. In a food context, squirrel monkeys monitor conspecifics more frequently than cooperative tamarin monkeys (Caine & Marra, 1988). Conversely, the provision of more feeding trays increases squirrel monkeys' social monitoring (Caine & Marra 1988).

Despite suggestions for a role for competition in social monitoring, few data demonstrate that social monitoring increases in larger groups of primates. The only study of this question reported a weak effect of group size on social monitoring (Treves, 1999). Therefore the influence of competition on social monitoring appears highly variable.

Mating competition

Increased male social monitoring during mating periods is thought to be a response to increased competition (Treves, 1999). However, the presence of receptive females almost certainly increases social monitoring by males (Keverne et al., 1978; Treves, 1999). High rates of social monitoring (Keverne et al., 1978) and vigilance (Yamamoto, 2005) in estrous females may be related to mate choice. Documentation of the target of monitoring would clarify whether social monitoring during mating periods reflects competition, mate choice or both.

Additional social influences on social monitoring

Sex differences

Sex differences in social monitoring have rarely been examined. Current data suggest males and female engage in similar frequencies of social monitoring (Keverne et al,. 1978; Pannozzo et al., 2007; Strayer & Gariepy, 1986). However, in some groups, females monitor conspecifics more frequently than males (Blois-Heulin & Girona, 1999). In studies of inferred social monitoring, males and females are equally vigilant (Alberts, 1994; Hirsch, 2002), although sex differences may vary as a function of context (Chalmeau et al., 1998).

These findings are interesting as male primates are usually dominant over females due to large size (Smuts, 1987). Accordingly, if rank influences social monitoring, then higher frequencies of social monitoring may be expected in female primates compared to males. Species differences may account for sex differences in social monitoring. Specifically, individuals in female- and male-bonded societies may differ in frequencies of social monitoring and according to the social relationships they possess within the group.

Proximity

It seems intuitive that proximity is related to social monitoring. Do primates monitor conspecifics that are closer, or would proximity (and perhaps aspects of peripheral vision) negate the need to monitor close associates? Pitcairn (1976) suggested that macaques which had frequent contact rarely looked at each other. However, examination of his matrices indicated this

was certainly not the case for all individuals, especially males. Strayer and Gariepy (1986) identified that affiliative and cohesive behaviours were associated with closer-range social monitoring, while no consistent or stable behavioural basis was evident for more distant monitoring.

Studies have also provided inconsistent results of the effects of nearest neighbours on vigilance. A social monitoring explanation for vigilance is commonly inferred if vigilance increases with the number of neighbours. Close neighbours may facilitate increased vigilance (Hirsch, 2002; Kutsukake, 2006; 2007) or reduce vigilance (Hill & Cowlishaw, 2002; Treves et al., 2001). Nonetheless proximity is important for interpreting social monitoring. Knowing the spatial location of conspecifics that are monitored, will help strengthen the case for relationship quality on social monitoring as proximity is one of the best indicators for social relationships (Cords, 1997; Silk, 2002).

Are different types of visual attention used to monitor conspecifics?

The type of visual attention used to monitor has rarely been considered in studies of social monitoring or vigilance. The use of glances (rapid visual attention) is usually associated with nervousness (Mitchell, 1972). Detailed studies by Blois-Heulin and colleagues have provided evidence for variability in attention types as a function of context, competition, status and food dispersion. Rapid glances are more likely to be used to monitor conspecifics: a) when preferred food is present (Blois-Heulin & Girona, 1999); b) by individuals in hierarchically organised groups, particularly young females (Blois-Heulin, 1999); and c) and when food is clumped rather than dispersed

(Blois-Heulin & Martinez-Cruz, 2005). In contrast, longer lasting looks occur more frequently during non-food contexts (Blois-Heulin & Girona, 1999) or when food is dispersed (Blois-Heulin & Martinez-Cruz, 2005). This variability in visual attention types, suggests that during feeding, glances are used in response to feeding competition and/or in response to demands on attention.

The stability of social monitoring

The evidence presented so far suggests that social monitoring is responsive to changes within the group such as competition and mating periods. Frequencies of social monitoring change when group composition varies: a) when a potential competitor emigrates from the troop (Jack, 2001); b) the arrival of a new infant (Blois-Heulin & Martinez-Cruz, 2005); c) in response to rank status changes (Keverne et al., 1978); and d) in response to estrous females (Keverne et al., 1978; Treves, 1999).

Therefore it is likely that studies of social monitoring only provide a 'snap-shot' of visual attention in response to social events occurring at a given time. Unfortunately, long-term studies of social monitoring are lacking.

Thesis overview

The review of the existing literature suggests that many avenues in social monitoring research still need to be explored. Social monitoring is more complex than previously thought, in that social monitoring may be related to a number of conspecific influences such as agonism, affiliation, competition, proximity, and by individual factors such as sex and rank status. Most importantly, social influences on monitoring can only be fully examined if

monitoring is considered as a dyadic behaviour, which involves accounting for both the initiator and receiver of monitoring. The way forward concerns a dyadic approach to social monitoring rather than the traditional individual-level approaches. Accordingly, within a dyad, relationship quality can be assessed, and the exchange of attention within a dyad can be measured in terms of whether A monitors B as equally as B monitors A, or whether one individual within a dyad is primarily responsible for social monitoring.

To gain a more complete picture of social monitoring, additional influences on social monitoring such as the behavioural context, species, and visual budgets need to be compared in concert with social variables.

Selection of study species

Given the remarkable diversity in the genus Primates, the study species of chimpanzees, orang-utans, siamangs, baboons and ring-tailed lemurs were selected on a number of factors. The first was taxonomic class, with at least one study species representing great apes, lesser apes, monkeys and prosimians. Accordingly, principles of social organisation such as multi-male species, monogamous species and semi-solitary species were reflected in the choice of taxonomic comparisons. Social organisation may be useful in considering the influence of competition and social bonding on visual attention. One-male groups were not considered, as some knowledge exists of social monitoring in these groups (Dunbar, 1983; Emory, 1976ab; Watts, 1998) coupled with evidence that attention is predominantly focused on the adult male. Within species, it was deemed important to include primates that have not been studied before. Accordingly, knowledge on visual attention is

particularly sparse in apes and prosimians.

It was not possible to study all these species in a non-captive environment; however, for some control of environmental factors all the apes were studied in captivity. Captive baboons and ring-tailed lemurs tend to be more aggressive than those observed in the wild, indeed because female lemur aggression can be severe, many exhibits of *Lemur catta* feature only bachelor groups (personal observation). Therefore, free-ranging lemurs and baboons were studied. These species also provided additional comparisons such as the effect of predators in female bonded, multi-male groups.

Thesis outline

Assessing social relationships and social monitoring

Chapter 2 describes the detailed methodology utilised for assessing relationship quality and social monitoring in five primate species.

Relationship quality and social monitoring

In chapters 3-5, I focus on the influence of social relationship within dyads and how these relationships influence social monitoring, both in terms of the frequency and the patterning of attention in all the study species. Social relationships are assessed using affiliative, agonistic and rank relationships, to gauge the primary influence of social monitoring.

Additionally in chapter 3, I address the stability of social monitoring over two behaviourally distinct seasons in ring-tailed lemurs. In chapter 4, the symmetry of monitoring in baboon dyads is examined as a function of the social relationship and dyad composition. Chapter 5 is a comparative test of

the assumptions of the attention structure theory (Chance, 1967; Chance & Jolly, 1970) in captive apes.

Social monitoring as information seeking

In chapter 6, I evaluate the role that monitoring conspecifics may serve in the context of social referencing. Social referencing usually occurs in ambiguous situations, so visual reference of conspecifics may allow an individual to respond appropriately based on the referent's behaviour. In this chapter, social referencing in response to naturally occurring events and in response to playback vocalisations is quantified to identify the effect of novelty, familiarity and biological relevance on visual referencing behaviours.

A unifying explanation for social monitoring and its role with vigilance

Chapter 7 documents the visual budgets of the study primates and addresses the influence of context on social and non-social attention. The use of glances and looks is evaluated in terms of reflecting within-group competition and/or attention constraints. Finally, data collected from previous chapters on all species are used to evaluate whether a single predictor or combinations of predictors of social monitoring can be identified and are applicable to different contexts and species. In this chapter, I aim to provide a unifying explanation and account for social monitoring in primate groups.

CHAPTER 2

METHODOLOGY FOR ASSESSING SOCIAL BEHAVIOURS AND SOCIAL MONITORING

Overview

In this chapter, I document details and the rationale of the data collection protocols for social monitoring and social relationships (chapters 3-5 and chapter 7). Information on the total number of focal animal samples collected for each species is documented here. The assessment of relationship quality and details about matrix permutation tests that permit non-independent data to be analysed are detailed. The methodology for social referencing is described in chapter 6.

Data collection protocols

Data were collected using check-sheets with a detailed coding system. Two behavioural protocols were used to sample social behaviour and visual attention. Each group member was selected for a five-minute (15-minute focal periods for the orang-utans) focal animal sample (Altmann, 1974) at least once per day based on ease of visibility. Roughly equal numbers of morning and afternoon focal samples were collected for both the protocols.

Attempts were made to ensure that at least four hours of data (48 five-minute focal animal sessions) were collected per focal individual for each protocol. Table 2.1 presents information on the number of focal samples collected for each species.

Social behaviour protocol

The aim of this coding system was to obtain an overall picture of the group structure and to assess dyadic social relationships in terms of the frequency of dominance related behaviours, agonistic and affiliative behaviours. All occurrences of aggressive and submissive interactions involving the focal individual were collected throughout the five-minute focal period. All occurrences of affiliative interactions such as grooming and contact were also collected. Point sample data were collected every minute during the focal period to document the nearest neighbour within five metres and the activity of the focal animal: resting, feeding, moving, grooming, or other activity not listed.

Visual attention protocol

The visual attention protocol was used to categorise visual attention and account for visual attention even when social monitoring was not occurring. Pilot work determined the most optimal sampling strategy for visual attention: 10-second point samples, for a maximum of five minutes. Data on social behaviour were not collected concurrently, in line with other studies of visual attention in primates (e.g. Pannozzo et al., 2007)

Focal observations were conducted on each group member to record the state of visual attention. Cross category point samples of visual attention (detailed below) were taken every 10 seconds within the focal sample. Each individual was observed for five minutes (terminated if the focal was out of view > 1 min) resulting in 30 point samples of attention per focal sample.

At each 10-second point, one of three mutually exclusive and exhaustive attentional states was coded: occupied attention, passive attention and vigilance. The context of the focal animal was also recorded: feeding, resting, allogrooming, autogrooming, moving and other not listed contexts.

1. Occupied attention

Occupied attention was scored when a focal animal was not attentive to the group or environment.

a) Eyes closed - the focal animal's eyes were closed.

b) Head down - the focal animal's head was orientated downwards. This usually occurred during resting, or as recipient of grooming.

c) Task orientated attention - attention was directed towards a task the focal animal was engaged in. Task orientated attention occurred when attention was directed towards foraging, processing and manipulating food, when picking through the hair and skin while self grooming or allogrooming.

2. Passive attention

Passive attention was scored when the focal animal's attention was unoccupied, and the head was orientated forwards but remained stationary.

3. Vigilance

A focal animal was scored as vigilant, when their head and/or eyes were re-orientated to a conspecific or to the environment. If vigilance was scored, additional information was collected.

i) Attention type

a) Glance - rapid, brief eye movement often accompanied by quick orientation of the head, lasting less than one second in duration.

b) Look - head and/or eye orientation lasting longer than one second.

c) Other - attention type not listed.

ii) Target of vigilance

a) Social - attention was directed towards a conspecific within the same group (social monitoring).

This code excluded attention towards a social partner that the focal animal was interacting with e.g. a grooming partner.

b) Non-social - attention was directed towards a non-social target.

This code included attention directed outside the social group e.g. extra-group conspecifics. Attention to food or securing resources was scored as task orientated attention not non-social monitoring.

iii) Proximity of social target

When social monitoring was scored, the proximity of the target was documented. The aim was to distinguish between close proximity and

more distant proximity categories, considering greater than five meters to be possibly outside of immediate visual range.

a) Close proximity - social target of attention was less than one metre away from the focal individual

b) Distant proximity - social target of attention was between one and five metres from the focal individual

c) Not in proximity - social target of attention was greater than five metres away from the focal individual.

4. Unknown attention

The state of attention was unable to be determined.

Table 2.1 The number of 5-minute focal samples collected using the social protocol and number of 10-second visual attention point samples for each species.

Species	# social focal samples	# visual 10-sec point samples
Chimpanzee	95	2418
Siamang	103	2475
Orang-utan	21*	1880
Lemur birth season	60	1806
Lemur mating season	61	1839
Baboon	41	1197

* 15-minute focal samples

Assessing social relationships

Dominance ranks were computed by summing agonistic interactions including contact aggression, non-contact aggression, submissive behaviours and displacements collected using the social protocol. Based on

the winner-loser outcome of aggressive interactions, the most dominant individual was assigned a rank of one, and lower ranking individuals were assigned lower values of ranks consecutively. Rank difference between individuals was also calculated, so individuals with adjacent rank positions possessed a low rank difference score, and individuals with disparate rank positions possessed a high rank difference score.

Dyadic rates of agonism were computed by adjusting the frequency of aggressive interactions by total time observed for both individuals. The rate of receiving aggression from partners was also calculated similarly. Each individual also had an overall rate of aggression received from all conspecifics within the group calculated.

Dyadic affiliative relationships using the focal social data were assessed using one of two sociality indices: Silk and colleague's sociality index (Silk, Altmann & Alberts, 2006a) or the dyadic association index (Cairns & Schwager, 1987). The choice between the indices was based on their previous use with particular species. An individual's rate of participation in affiliative interactions (as either a recipient or initiator) was calculated by summing the frequency of interactions, adjusted by time observed.

Indices of affiliative relationship quality

Sociality index

This index uses the frequency each dyad spends grooming and in proximity to each other to assess the strength of positive social relationships. For each dyad, the number of point samples using the social protocol in which dyad members were grooming and the number of times they were nearest

neighbours was divided by the frequency of point samples that the dyad partner was present in the group. The proximity (Pij) and grooming frequencies (Gij) (corrected for partner availability) were then divided by the mean frequency of proximity (Pxy) for all dyads in the group and the mean frequency of grooming (Gxy) for all dyads within the group.

$$\left(\frac{\frac{Gij}{Gxy} + \frac{Pij}{Pxy}}{2} \right)$$

The sociality index equation (Silk et al., 2006a) results in a score that indexes the extent to which each dyad deviates from the average of all dyads. Furthermore, a 95% confidence interval was calculated around the mean sociality index value. Dyads that scored above the 95% confidence interval of the mean were classed as possessing a strongly affiliative relationship, i.e. friends.

In this thesis, this index was used to assess social relationships in baboons and ring-tailed lemurs. The index developed for baboons (Silk et al., 2006a) was deemed appropriate to use in lemurs, as it takes into account both frequencies of grooming and proximity, important measures of good relationships in lemurs (e.g. Kappeler, 1993; Nakamichi & Koyama, 1997). As sample sizes were large, sociality index scores were calculated separately for female-female, male-male and male-female dyads. Additionally, because each dyad was weighted against the mean values of grooming and proximity of the troop, high values on this index represented dyads that possessed stronger bonds than the average dyad.

Dyadic association index

The nearest neighbour data of chimpanzees, orang-utans and siamangs was used to calculate a simple ratio index (Cairns & Schwager, 1987). This index uses information on time spent in proximity: the number of point samples in which A is the nearest neighbour of B, compared to time when A is not the nearest neighbour of B. This index was appropriate to use with orang-utans as it takes into account the nearest neighbour within five metres rather than grooming, which was not appropriate because grooming occurs rarely in captive orang-utans (Maple, 1980). Because, data on chimpanzees, siamangs, and orang-utans were compared together in chapter 5, it was necessary to use an index that was appropriate for all these apes. The dyadic association index has previously been used to assess relationships in chimpanzees (e.g. Boesch & Boesch-Achermann, 2000; Kutsukake, 2006). Hence, all dyads received an association score that indicated the strength of the social relationship based on time spent in proximity.

Calculating visual attention

Visual budgets for individuals within each species were calculated to account for percent of visual time that attention was scored as occupied, passive or vigilant. The number of 10-second point samples for each mutually exclusive and exhaustive attention code, was divided by the total number of 10-second point samples collected. In this thesis, the term vigilance is used to define re-orientation of the head and/or eyes towards any target. The terms social and non-social monitoring specifically pertain to vigilance towards a social or non-social target respectively.

Calculating social monitoring

Social monitoring data were first summarised for each dyad. The frequency of monitoring within a dyad (A monitoring B, and B monitoring A) was divided by the total time observed for both individuals to give a rate of monitoring per hour for the dyad. At an individual level, the focal animal's overall rate of social monitoring was summarised into rate per hour by dividing the frequency of total social monitoring (all conspecifics within the group) with the observed time of the focal animal.

Analysing social monitoring

Matrix correlation analyses (Noldus MatMan v1.1) were used to assess the influence of dyadic relationship quality on social monitoring. The Mantel test is a matrix permutation program that calculates several indices of association between variables from observed dyadic values, and then randomly permutes row and column values to generate sampling distributions against which to assess the significance of test statistics derived from the original data matrix (de Vries et al., 1993). This test avoids problems associated with non-independence of dyads (de Vries et al., 1993; Hemelrijk, 1990).

To test hypotheses that social monitoring was related to social relationships, a matrix of social monitoring was correlated with matrices containing sociality index scores (or dyadic association scores); rates of agonism, and rank difference. Mantel's Z and Zr tests and Pearson's r statistics were used, with matrices permuted 2000 times.

To aid comparison with previous studies of social monitoring, some additional analyses were conducted at the individual level. These involved

analyses of variance, bivariate correlations and t-tests. These tests are described in the relevant chapters.

CHAPTER 3

SEASONAL INFLUENCES ON SOCIAL MONITORING IN FREE-RANGING RING-TAILED LEMURS (LEMUR CATTA)

Overview

In this chapter, I take a first look at patterns of social monitoring in a free-ranging prosimian species and evaluate the stability of social monitoring across two behaviourally distinct seasons. Study 1 concerns social monitoring during the birth season with reference to the social relationships between dyads. Study 2 examines social monitoring in the mating season, a time of increased agonism and competition. I also evaluate whether social relationships remain stable across seasons and how this stability or instability affects patterns of social monitoring particularly with reference to sex differences.

Dissemination of research from this chapter

Lane & Bard (2007). Seasonal influences on visual social attention in free-ranging ring tailed lemurs. Oral presentation at the American Society of Primatologists meeting, June 17-20, North Carolina, USA.

Lane & Bard (2008). Assessing dyadic social attention in *Lemur catta*. Oral presentation at the International Primatological Society meeting, August 3-8, Edinburgh, UK.

Lane, Bard, Reddy & Jolly (under revision). An affiliative basis for visual social monitoring in ring-tailed lemurs at Berenty reserve, Madagascar. International Journal of Primatology.

Introduction

Studies of visual attention in primates focus on vigilance directed outside of the social group, which serves an important anti-predatory function (Elgar, 1989; Lima, 1994; Pulliam, 1973; Treves, 2000). Vigilance towards extra-group and intra-group conspecifics is likewise seen primarily as threat protection, e.g. protecting mates and resource defence against competitors (Baldellou & Henzi, 1992; Gould et al., 1997; Rose & Fedigan, 1995), protecting against the risk of infanticide (Steenbeek et al., 1999) and avoidance of agonism from dominant animals (e.g. Chance, 1967). Within a social group, attention towards conspecifics is thought to vary in accordance with the level of conspecific threat (Treves, 2000). Low-ranking individuals are reported to monitor more frequently than high-ranking individuals (Caine & Marra, 1988; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998; Pannozzo et al., 2007) and individuals that receive higher rates of aggression appear to monitor at higher rates (Keverne et al., 1978; Pannozzo et al., 2007). However, rank influences on attention are not consistent between species (e.g. Torres de Assumpção & Deag, 1979).

Vigilance towards potential aggressors or high-ranking conspecifics is undoubtedly important. Gorillas watch adversaries more than associates (Watts, 1998) and long-tailed macaques monitor infrequent interactants more than familiar conspecifics (Pitcairn, 1976). However, it seems unlikely that threat protection is the only influence on within-group attention: at the least, the importance of threat protection will vary across primate species. Affiliative interactions in primates occur frequently, in contrast to agonistic interactions (Sussman et al., 2003; 2005). There is evidence that affiliation may play a

role in social monitoring. Squirrel monkey dyads that exchange visual attention are more often engaged in affiliative, rather than dispersive or agonistic activity (Strayer & Gariepy, 1986). In female gelada baboons, attention is directed towards female allies, in addition to the male (Dunbar, 1983). High rates of attention are also directed towards play partners (Emory, 1976b). Therefore, intra-group vigilance may reflect (at least) two different motivational states: monitoring may underlie avoidance of aggression, as well as monitoring friends (Dunbar, 1988).

Visual attention in lemurs

Lemurs are an appropriate species to assess the effects of social influences on visual attention. First, vigilance is important for lemurs in terms of detecting predators and conspecifics outside the group (Gould, 1996a; Gould et al., 1997; Lewis, 2005; Overdorff, 1998; Rasolofoson, 2003; Sauther, 1989). Ring-tailed lemurs engage in frequent visual social monitoring of conspecifics within the group (Shepherd & Platt, 2008). Finally, the social organisation of ring-tailed lemurs allows several hypotheses to be tested about the behavioural correlates of social monitoring.

In ring-tailed lemurs, females are dominant to all males (Jolly, 1966; 1984; Jolly et al., 1993; Kappeler, 1990; Pereira, Kaufmann, Kappeler & Overdorff, 1990; Sauther, 1993). Therefore, if monitoring were related to only subordinate status, then all males would have higher rates of monitoring conspecifics than females. Within-troop aggression in ring-tailed lemurs can be severe (Jolly, 1966; Kappeler, 1993; Pereira & Kappeler 1997; Vick & Pereira, 1989); however, the frequency of agonistic and affiliative behaviours

in *Lemur catta* varies as a function of relationship quality and sex composition within dyads. Lemurs do not distribute grooming or associate evenly across all troop members. Close proximity and high frequencies of grooming are indicative of good relationships within dyads (Jolly, 1998; Kappeler, 1993; Nakamichi & Koyama, 1997; Overdorff, 1998; Pereira & McGlynn, 1997; Taylor & Sussman, 1985). Kappeler (1993) reported that female-female ring tailed lemurs' social relationships were almost wholly affiliative or agonistic. In contrast, male lemurs receive similar rates of aggression from female friends compared to female non-friends (Gould, 1996b).

Based on this knowledge of social relationships in ring-tailed lemurs, if there is a relation between social monitoring and dyadic qualities, then it is expected that monitoring may differ according to the sex of the initiator; the sex of the target individual; and the relationship between them. These issues have not been examined fully in either anthropoids or prosimians.

Typically, studies of social monitoring focus on an individual level of visual monitoring i.e. overall rate of monitoring, and do not consider the target identity. However, it is important to consider social monitoring of dyads because it is predicted that the relationship between partners in a dyad will influence patterns of monitoring.

Predicting social monitoring in lemurs as a function of social structure

If the monitoring of affiliatives is a primary factor influencing social attention, then different patterns should be evident for male and female lemurs, and friendly and non-friendly dyads. First, female lemurs are expected to be the

target of monitoring more frequently than male lemurs due to the females' central role in the troop (e.g. Jolly, 1966). Secondly, it is predicted that strong affiliates or friends will be monitored more frequently than non-friends. Third, an interaction is predicted between affiliative status and sex. Specifically, female lemurs should monitor most often those partners with whom they possess strongly affiliative relationships i.e. female friends. Although females form friendships with males (Gould, 1996b), a female-female friendship is hypothesised to be more valuable for ring-tailed lemurs due to their female dominant organisation. As male-male relationships may be important for emigration (Gould, 1997; 2006) and male-female relationships for gaining access to the central female core (Gould, 1996b), monitoring in males is expected to be directed towards both female and male friends.

If an agonistic basis for monitoring exists, then dyads with an agonistic relationship should engage in more frequent rates of monitoring than those with an affiliative relationship. Specifically, both females and males should attend to adversaries, and the strongest adversaries will be females given the female dominant structure of ring-tailed lemurs (e.g. Jolly, 1984; Kappeler, 1990; Sauther, 1993). If Chance and Jolly's (1970) theory on rank based attention structure is applicable to lemurs, then all males should engage in more frequent monitoring than females due to all males' unconditional subordinate role.

The role of proximity in social monitoring

Proximity of the target of monitoring may be an important factor to consider in social monitoring studies. Close proximity is indicative of good

relationships in ring-tailed lemurs (Kappeler, 1993; Nakamichi & Koyama, 1997; Taylor & Sussman, 1985). Accordingly, it is predicted that friends will be monitored in a closer proximity category than non-friends. It is expected that if non-friends are monitored, they would be monitored at a greater distance than friends. An interaction of sex with proximity is predicted: females are spatially central in *Lemur catta* (Jolly, 1966) so the influence of proximity will be more variable for males than it is for female lemurs.

The goal of this study is to take a first look at the influence of social relationships on visual monitoring in one group of free-ranging prosimians to determine if patterns of monitoring reflect social structure. The specific aims of the study are threefold: a) to classify affiliative social relationships in ring-tailed lemurs; b) to evaluate the extent to which the traditional attention structure theory fits in with social monitoring in lemurs; and c) to test the influence of social behavioural correlates (affiliation, agonism and rank) on the frequency and patterns of social monitoring within lemur dyads.

STUDY 1: SOCIAL MONITORING DURING THE BIRTH SEASON

Methods

Study site

The study was conducted at Berenty private reserve in Southern Madagascar. The 200-ha reserve comprises four main habitats: front zone, gallery forest, transitional scrub and spiny desert (Jolly, Koyama, Rasamimanana, Crowley & Williams, 2006). The study took place in the front habitat dominated especially by endemic *Tamarindus indica* and *Rinorea*

greveana and by non-native plants such as eucalyptus *sp.* and *Azadirachta Indica* (Jolly et al., 2006; Rasamimanana & Rafidinarivo, 1993; Soma, 2006).

Study species and subjects

Adult and subadult members (N=14, 7 females, 7 males) of a front troop (troop YF) were observed from August to October 2005 (birth and lactation season, dry/winter period). An additional juvenile and a peripheral male were not focal animals, but featured as interactants. The troop was selected for study due to excellent visibility, consistent ranging patterns, high levels of habituation and representative troop composition, including two matrilines.

Data collection and analysis

Data collection protocols and the number of focal samples collected are summarised in chapter 2. Mantel tests were used to correlate matrices of social monitoring with dyadic sociality index scores, rates of agonism and rank differences. Parametric statistics were used to analyse data at the individual level. To aid comparison with previous studies, rank position was correlated with the overall frequency of social monitoring. Related t-tests compared rates of agonism received from friends compared to non-friends. A mixed repeated measures ANOVA (focal sex x relationship quality x target sex x proximity) was employed to determine: a) if lemurs preferentially monitored friends compared to non-friends; b) if monitoring friends differed in males and females; c) if monitoring varied according to the target's sex; and d) if monitoring was influenced by target proximity. Significant ANOVA results were followed up with selected adjusted post hoc tests.

Results

Visual attention budgeting

Approximately 33% of lemurs' visual attention was spent actively monitoring the environment and conspecifics. Specifically, social monitoring occurred exclusively for 9% of the visual budget and 24% of visual time was spent monitoring outside the troop. Female and male lemurs spent equal time vigilant: $t(12) = 0.098$, $p = 0.924$.

Relationship quality and social monitoring

Affiliative relationships

The majority of lemurs possessed weak social relationships, with sociality index scores of less than one (see Figure 3.1 for the distribution of sociality index scores). Only dyads scoring above the 95% confidence interval of the sociality index mean were classed as having a strong affiliative relationship. Out of 105 dyads, 26 dyads were considered friends.

The relation between sociality index score and monitoring

Sociality scores were significantly correlated with social monitoring (Mantel Z: 546.3, $r = 0.45$, $p = 0.001$). Specifically, the higher the sociality index score in a given dyad, the higher the rate of social monitoring.

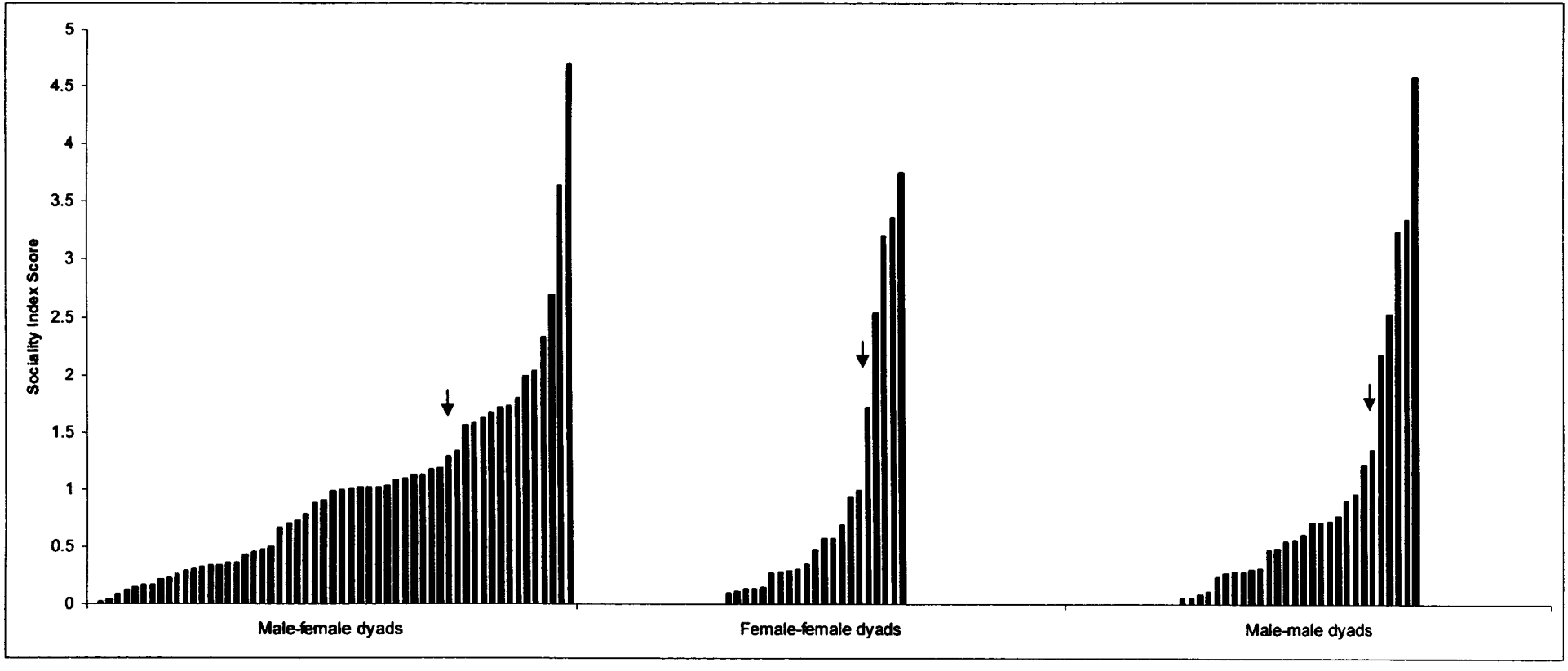

Figure 3.1 Distribution of sociality index scores in ring-tailed lemurs detailing each dyad within male-female, female-female and male-male classes.

↓ denotes the point at which sociality scores were greater than the 95% confidence interval of the mean, i.e. friend dyads.

Moreover, a significant relation between sociality scores and visual monitoring was found for all types of dyads (Figure 3.2). Female-male dyads (Mantel Zr: 133.6, r = 0.59, p = 0.001), female-female dyads (Mantel Z: 227.5, r = 0.67, p = 0.001), male-female dyads (Mantel Zr: 32.5, r = 0.26, p = 0.046), male-male dyads (Mantel Z: 107.9, r = 0.42, p = 0.049).

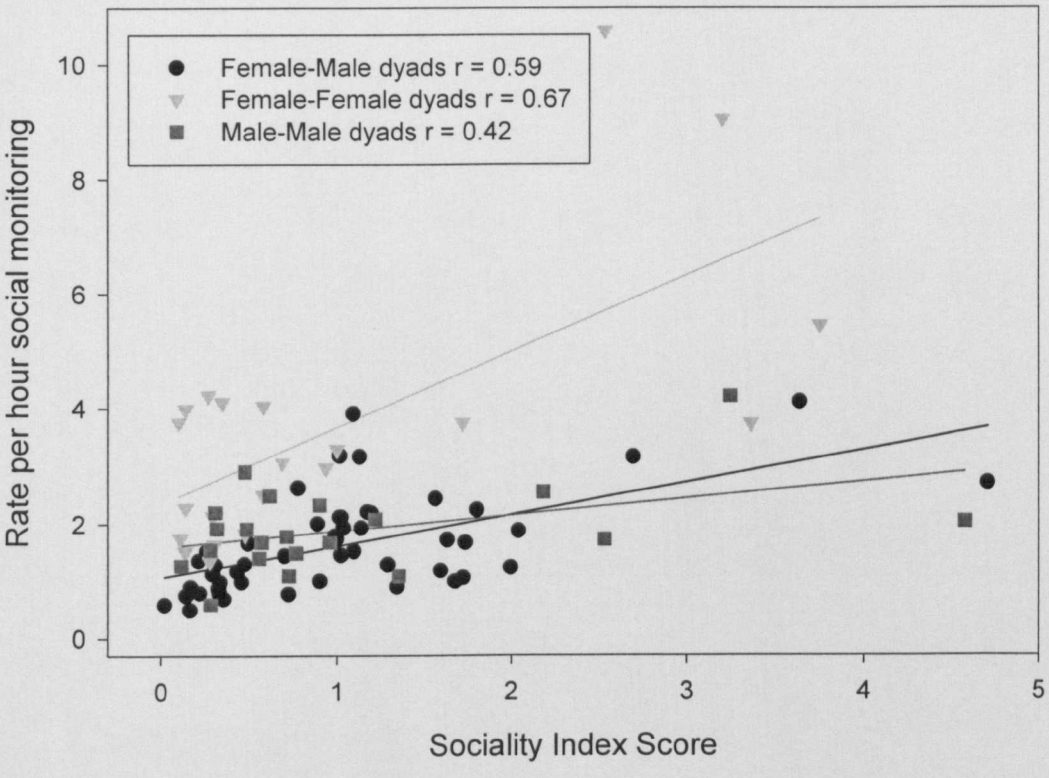

Figure 3.2 The relation between sociality index score and social monitoring in ring-tailed lemurs.

Agonistic relationships

Agonism occurred most frequently in female-female dyads, at a rate of 0.56 per hour. Lower rates of agonism occurred in male-male dyads (0.28/hr), and in male-female dyads (0.20/hr). Males received similar levels of aggression from male non-friends compared to male friends: t(6) = 0.90, p = 0.393, and

from female friends compared to female non-friends: t(6) = 1.229, p = 0.265. However, females received less aggression from female friends compared to female non-friends: t(6) = 2.549, p = 0.022.

The relation between rank position, agonism and social monitoring

Visual monitoring of conspecifics was not correlated with rates of agonism (Mantel Z: 143.2, r = 0.13, p = 0.112) or the rank difference within dyads (Mantel Z: 1854.4, r = -0.15, p = 0.893). Using the same analysis as previous studies, the rank position of a lemur and their individual rate of social monitoring were not related: (n =14), r = -0.23, p = 0.425. Thus, neither dominance rank nor agonism was related to visual monitoring in this troop of lemurs.

Sex differences, relationship quality and targets of social monitoring

There was a significant three way interaction of focal sex x target sex x relationship quality: F(1,11) = 7.917, p = 0.017 (Figure 3.3). Females monitored female friends significantly more than males monitored female friends: t(11) = 3.3462, p = 0.005 and males monitored male non-friends significantly more than the females monitored male non-friends: t(11) = -4.494, p= 0.001. However, males and females were equal when the targets of monitoring were female non-friends: t(11) = 0.737, p = 0.477 and male friends: t(11) = -1.817, p = 0.097.

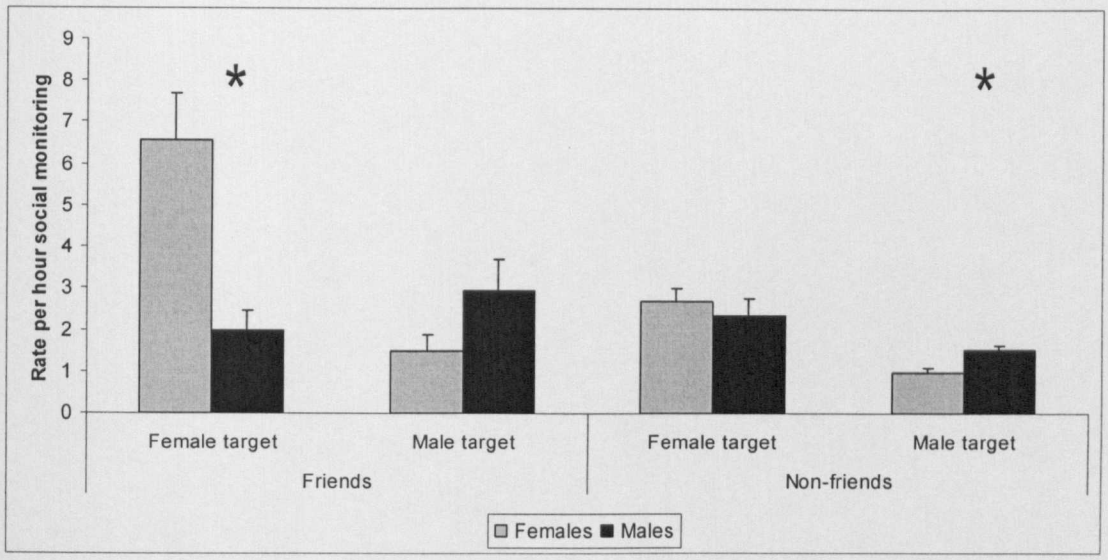

Figure 3.3 Social monitoring of friends and non-friends by male and female ring-tailed lemurs.

All two-way interactions pertaining to focal sex were significant, supporting strong differences between rates of monitoring for males and females as a function of relationship quality: $F(1,11) = 4.948$, $p = 0.048$ and sex of the target: $F(1,11) = 13.455$, $p = 0.004$. Females monitored friends (8.1/hr) significantly more than non-friends (3.7/hr): $t(6) = 3.658$, $p = 0.011$, while males monitored friends (4.9/hr) and non-friends similarly (3.9/hr): $t(5) = 1.320$, $p = 0.244$. Females monitored female targets significantly more than male targets: $t(6) = 5.362$, $p = 0.002$, while males monitored female and male targets equally: $t(5) = -0.113$, $p = 0.914$. There was no significant interaction of target sex by relationship quality: $F(1,11) = 0.731$, $p = 0.411$.

All ANOVA main effects were significant but the higher order interactions indicated that the main effects of sex: $F(1,11) = 5.754$, $p = 0.035$; relationship: $F(1,11) = 13.225$, $p = 0.004$ and target sex: $F(1,11) = 12.241$, $p = 0.005$ varied according to the levels of the other factors.

The influence of proximity on social monitoring

Proximity was significant in a three-way interaction with focal sex and relationship quality: $F(2,22) = 3.438$, $p = 0.050$. Female lemurs (significantly more than the males) monitored friends in distant proximity: $t(11) = 2.337$, $p = 0.039$ and monitored friends in close proximity: $t(11) = 2.465$, $p = 0.031$ (Figure 3.4). Males and females equally monitored friends that were not in proximity: $t(11) = -0.431$, $p = 0.675$ and non-friends in all proximity categories.

The remaining three-way interactions were not significant. Relationship quality was not influenced by proximity: $F(2,22) = 3.180$, $p = 0.061$; however, the influence of proximity on social monitoring varied as a function of focal sex: $F(2,22) = 4.167$, $p = 0.029$ and target sex: $F(2,22) = 3.715$, $p = 0.041$. Females monitored significantly more than the males when the target was in distant proximity: $t(11) = 2.339$, $p = 0.039$ or in close proximity: $t(11) = 2.401$, $p = 0.035$. Males and females were equal in monitoring targets not in proximity: $t(11) = -0.698$, $p = 0.499$.

Female rather than male targets were more likely to be monitored in distant: $t(12) = 2.457$, $p = 0.030$ and close proximity ranges: $t(12) = 2.457$, $p = 0.024$. However, when not in proximity, male and female targets were monitored equally: $t(12) = 1.896$, $p = 0.082$. The main effect of proximity was significant: $F(2,22) = 43.795$, $p = <0.001$, but varied according to the levels of the other factors as documented above.

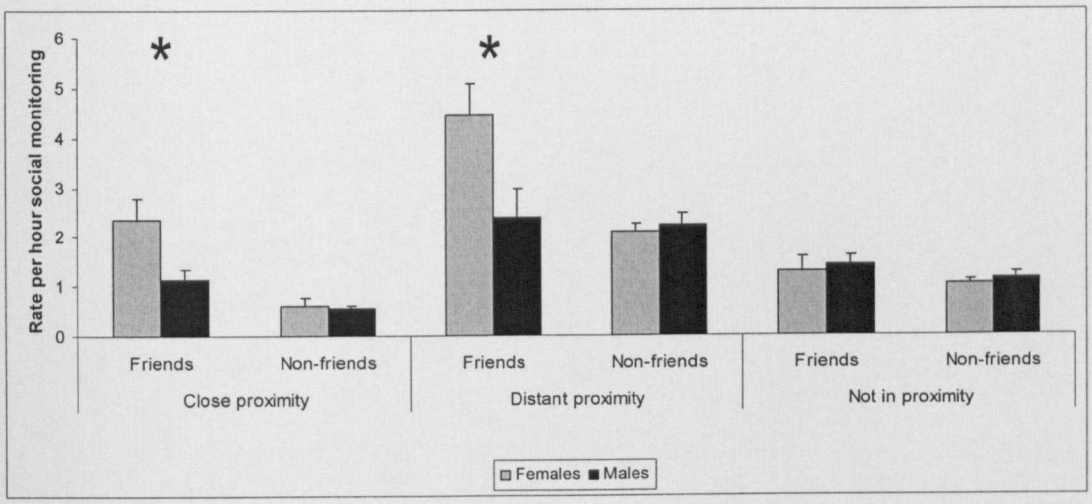

Figure 3.4 The influence of proximity on the monitoring of friends and non-friends in ring-tailed lemurs.

Discussion

An affiliative basis of social monitoring in Lemur catta

The results strongly support an affiliative basis for social monitoring in this troop of ring-tailed lemurs, based on sociality indices, absence of agonistic and rank influences, proximity measures and sex differences associated with visual monitoring. While social monitoring is usually associated with threat protection (e.g. Keverne et al., 1978; Pannozzo et al., 2007), the data from this study support research also reporting the absence of agonistic or rank influences on social monitoring (Dunbar, 1983; Strayer & Gariepy, 1986; Torres de Assumpção & Deag, 1979). Perhaps one reason for these results is due to the analysis of dyads rather than the usual analysis of individual level visual monitoring, which allows consideration of not only whether monitoring occurs, but most importantly the target of monitoring and other features of the dyadic relationship in order to interpret visual attention.

At the dyadic level, the strength of the affiliative relationship was correlated with the rate of social monitoring. Taken one step further, the attributes of both the initiator and the target of monitoring were related and reflected the social structure of the group.

Keeping track of friends - the importance for females

Overall, females attended to conspecifics more frequently than the males, and particularly female friends. This finding was supported by the additional information on proximity. Nearest neighbours in ring-tailed lemurs are often kin or friends (Kappeler, 1993; Nakamichi & Koyama, 1997; Taylor & Sussman, 1985), individuals of the same sex (Kappeler, 1993) or individuals that are infrequently opponents (Pereira & Kappeler, 1997). In the current study, females monitored female friends more often when in distant proximity. When targets were not in proximity, social monitoring decreased, and both friends and non-friends were monitored equally.

The female data provide support for Dunbar's (1988) suggestion that social monitoring may function in keeping track of female friends in the troop. Females preferentially monitored their friends and this may be related to the fact that in the study troop females received less aggression from female friends. Female-female relationships are unambiguous: they are either affiliative or agonistic (Kappeler, 1993) and of a long-term nature (Nakamichi & Koyama, 1997; Taylor and Sussman, 1985). Friendships in primates are thought to facilitate social bonding through grooming and proximity (Silk, 2002). However, in female dominant primates, females also benefit from collective defence against neighbouring troops or predators. Social

relationships in female ring-tailed lemurs may influence who participates in inter-troop encounters (Jolly et al., 1993; Nakamichi & Koyama, 1997; Nunn & Deaner, 2004) especially because females, not males, are the main instigators in these encounters. Maintaining good social relationships with other females may also function in the avoidance of targeted aggression that can lead to eviction from the troop particularly for young females (Vick & Pereira, 1989). Targeted aggression rarely occurs in friendly female dyads (Pereira & Kappeler, 1997).

Why male distribute attention more equally

In contrast to the predictions of the attention structure theory (Chance, 1967; Chance & Jolly, 1970), male lemurs monitored less frequently than the females and monitored all targets relatively equally. However, male monitoring was similar to the females when the target of monitoring was not in proximity, indeed the influence of proximity on social monitoring was less strong for the males. This suggests that male social monitoring is highly variable, especially as male roles in lemur troops may vary enormously. Newly immigrant males hold low-ranking, peripheral positions and face agonism from members of the troop (Gould, 1997; 2006). High-ranking and natal males spend more time nearer the female core (Jolly, 1966; Kappeler, 1993; Nakamichi & Koyama, 1997; Sauther, 1991; 1993; Sussman, 1991). It may be the case that male social monitoring represents two motivations: keeping track of both friends and adversaries in the group (Dunbar, 1988). This seems likely given that males did not receive less agonism from male or female friends. Although males may benefit from male-male friendships in

terms of establishing a male transfer partnership, these relationships are not of a long-term nature (Gould, 1997; 2006). Similarly, the benefits for males of maintaining visual contact with female friends are also unclear: males do not appear to benefit in terms of reduced aggression, mating advantages, female intervention in conflicts, or access to resources from friendships with females (Gould, 1996b). However, access to the central female core facilitated by male-female friendships may also necessitate the monitoring of both female friends and non-friends. If male social relationships are ambiguous, when similar levels of aggression are received from friends compared to non-friends (Gould 1996b) and males are more peripheral from the troop, then being socially vigilant towards both friends and non-friends may be an effective visual strategy.

STUDY 2: SOCIAL MONITORING DURING THE MATING SEASON IN COMPARISON TO THE BIRTH SEASON

There is little knowledge about the stability of social monitoring. However, social monitoring is known to be responsive to changes in social dynamics e.g. estrous periods and changes in alpha male status (Keverne et al., 1978). Ring-tailed lemurs are an ideal species to study for the variability of social monitoring because lemurs have (at least) two distinct behavioural seasons. The birth/lactation season (when most studies are conducted) is characterised by high rates of female competition during periods of relatively low food availability coupled with high energy demands of lactation (Rasamimanana & Rafidinarivo, 1993; Sauther, 1991; 1993). In contrast, the mating season in ring-tailed lemurs has been described as socially chaotic

(Jolly, 1966) with male-male aggression increasing enormously during mating season (Gould, 1997; Jolly, 1966; Koyama, 1988; Pereira & Weiss, 1991; Sauther, 1991; Sauther & Sussman, 1993; Taylor & Sussman, 1985).

The mating season is also associated with other behavioural changes especially for male ring-tailed lemurs. The male dominance hierarchy may break down (Jolly, 1966; Parga, 2006; Taylor & Sussman, 1985). However, this break down facilitates the separation of male competition from dominance, as aggression during mating season is associated with access to females rather than rank. Males tend to emigrate to new troops prior to the mating season (Gould, 2006; Sauther, 1991; Sussman, 1992), so male-male preferred partnerships or friendships generally do not persist through the mating season (Gould, 1997; Taylor & Sussman, 1985). Some male-female relationships can remain stable, with greater interindividual variability during mating season (Gould, 1996b). Female-male agonism may also increase in mating season, brought on by frequent male approaches towards females (Jolly, 1966; Koyama, 1988; Sauther, 1991). Sauther (1991) describes the monitoring of females by males through approaches, tail marking, tail waving, and by sniffing. However, the extent to which females are monitored visually is unclear.

Seasonal influences on social monitoring in ring-tailed lemurs

During the mating season, the function of monitoring conspecifics may change from keeping track of friends to functioning in the evaluation of potential mates for both males and females. Affiliative relationships could have less influence on who is monitored during the mating season for *Lemur*

catta, as Gould (1996b) reported that heterosexual friends did not mate. However, the stability of female-female relationships across seasons (Taylor & Sussman, 1985) indicates that female monitoring may remain at similar rates between seasons. Increased male aggression during mating season (e.g. Jolly, 1966b; Parga, 2006; Taylor & Sussman, 1985) means male social monitoring is likely to respond to changes in male-male competition (Treves, 1999).

Several predictions about the influence of seasonal changes on behaviour and the subsequent effects on social monitoring can be tested. Given that the mating season is characterised by high levels of male-male competition (Jolly, 1966; Parga, 2006; Sauther, 1991; Taylor & Sussman, 1985), it is predicted that rates of visual monitoring by males towards females increases in order to detect sexually receptive mates, and increases towards males to monitor competition. Because female social dynamics remain relatively stable across seasons, the affiliative basis of monitoring identified in study 1 is expected to persist across seasons for females. Because social monitoring cannot be studied in isolation from social behaviour, this study aims to answer several questions about the stability of social relationships between seasons, and whether seasonal changes in troop social dynamics influence social monitoring.

1. Do affiliative relationships persist over seasons or change in accordance with lemurs' strict reproductive seasonality?
2. If social relationships change, do overall rates of social monitoring also change from birth season through mating season?

3. Do the same behavioural correlates of social monitoring observed during birth season exist for mating season?
4. Do consistent patterns of social monitoring exist for males and females between seasons?

Methods

Data collection and analysis

Data from the birth season (study 1) were compared to new data collected during the mating season (April to May 2006) in the same troop of lemurs.

Table 3.1 Troop composition of ring-tailed lemurs.

Birth Season	Mating Season	Notes	Age class	Rank Position Birth	Rank Position Mating
Females					
AL	AL		Young prime	1	1
TU	TU		Prime	2	3
SC	SC		Prime	3	2
IS	IS		Prime	4	4
L2	L2		Subadult	5	5
PO	PO		Old	6	6
L1	L1		Subadult	7	7
-	TT	Not studied during birth season	Subadult	n/a	8
Males					
CH	CH		Prime	1	1
KI	-	Absent during mating season	Prime	2	-
PA	-	Emigrated T1B troop prior to mating season	Old	3	-
P1	-	Emigrated T1B troop prior to mating season	Young prime	4	-
P2	P2		Subadult	5	5
PM2	PM2	New immigrant in birth season	Prime	6	2
ST	-	Absent mating season	Old	7	-
-	PM1	Peripheral during birth season	Old	n/a	4
-	JF	New immigrant post birth season	Prime	n/a	3

See Table 3.1 for troop membership information for both seasons. In addition to the data collection protocols listed in chapter 2, during mating season, *ad libitum* data on copulations were collected. All occurrences of approaches and tail waving (a sign of sexual interest) were documented using the social protocol during the mating season.

Results

Correlations between behaviours at the dyadic level e.g. sociality scores, social monitoring, agonism and rank difference were analysed using the Mantel test as in study 1. Males and females were compared using t-tests.

Visual attention budgeting

Overall, social visual attention budgets increased significantly from birth to mating season (11% of visual time engaged in social monitoring during mating season): $t(9) = -2.847$, $p = 0.019$. During the mating season, males monitored conspecifics significantly more (12% of visual time) more than the females did (10% of visual time): $t(11) = -2.462$, $p = 0.032$.

Affiliative relationships

Stability of social relationships

Out of the 15 male-female dyads classified as friends in the birth season, one dyad remained as friends in the mating season and half were no longer friends because the male friend left the troop. No male-male friendships (zero of six dyads) observed in birth season persisted in the mating season. Female membership in the study troop remained stable across seasons, and

two of the six friendships observed in birth season remained friends in mating season.

Affiliation and social monitoring

During the mating season, the overall sociality index score was positively correlated with social monitoring (Mantel Z: 557.611, r = 0.37, p = 0.002). However, this positive correlation only applied to female-female dyads (Mantel Z: 198.1652, r = 0.45, p = 0.012) and female-male dyads (Mantel Zr: 32.0071, r = 0.35, p = 0.031). For male-male and male-female dyads, social monitoring and sociality scores in mating season were unrelated: male-male dyads (Mantel Z: 82.4258, r = 0.35, p = 0.176) and male-female dyads (Mantel Zr: 45.8418, r = 0.17, p = 0.173).

Mating behaviour

All mating that occurred during the day was observed. It is possible that mating also occurred at night, but in the morning, there was no evidence of new copulatory plugs in any females. All five adult females mated (one female mated with an extra troop male), as did all the males. Of the eight dyads that mated, seven were non-friends. Male-female friendships in this troop therefore did not directly benefit potential male reproductive success.

Sexual behaviour and monitoring

Males directed tail waving displays equally towards female friends (0.18/hr) and female non-friends (0.14/hr): t(4) = 0.511, p = 0.636. Tail waving to females did not occur in birth season, supporting the interpretation that the

behaviour is sexual in nature (Jolly, 1966; Koyama, 1988; Sauther, 1991). There was no indication that females especially monitored males that frequently waved their tails at them (Mantel Zr: 2.3844, r = 0.16, p = 0.31). There was also no relation between male tail waving and male monitoring of females (Mantel Zr: 7.3193, r = 0.22, p = 0.115).

Agonistic behaviour

The mating season was characterised by changes in levels of agonism especially in male-male dyads. Between females, agonism occurred at rates of 0.59 per hour, similar to that observed during birth season. Female to male rates of agonism increased from 0.20/hr in birth season to 0.45/hr in mating season. Male-male agonism increased almost four-fold, from a rate of 0.28/hr in birth season to a rate of 1.04 per hour during mating season.

Agonism and friendships

During mating season, male lemurs received equivalent levels of aggression from female friends compared to female non-friends: $t(4) = 1.643$, $p = 0.176$ and male friends compared to a male non-friends: $t(3) = -1.100$, $p = 0.352$. In contrast, females received less aggression from female friends compared to female non-friends: $t(7) = -5.359$, $p = 0.001$. These patterns of receiving aggression based on friendships were the same for birth season and mating season. Males did not benefit from friendships (in terms of reduced aggression) whereas females did.

Agonism and visual monitoring

During the mating season, agonism and social monitoring were positively correlated (Mantel Z: 317.4, r = 0.47, p = 0.0015, Figure 3.5). This correlation was particularly strong for male-female dyads (Mantel Zr: 43.6, r = 0.56, p = 0.008) and male-male dyads (Mantel Z: 93.3, r = 0.79, p = 0.036). There was no correlation between monitoring and agonism for female-female dyads (Mantel Z: 105.1, r = 0.28, p = 0.317) or female-male dyads (Mantel Zr: 5.03, r = 0.13, p = 0.130). In comparison, during birth season there was no relation between agonism and social monitoring for any dyads.

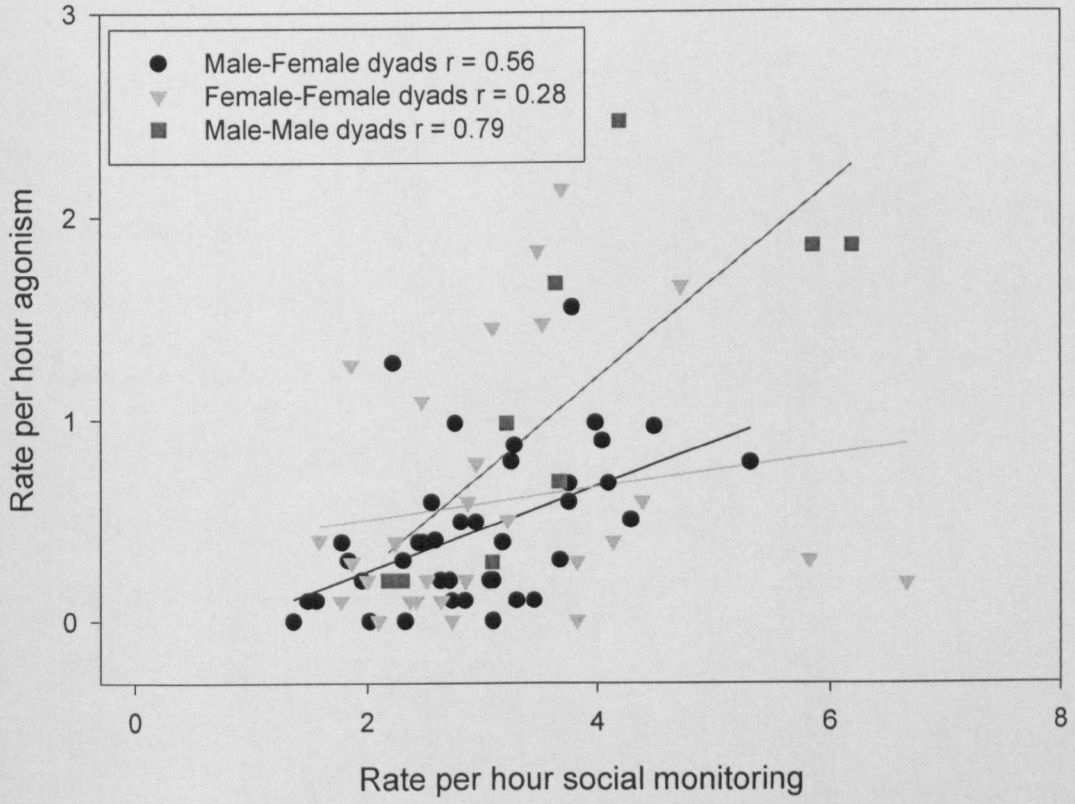

Figure 3.5 The influence of agonism on social monitoring in ring-tailed lemurs.

Rank position and social monitoring

In the mating season, the rank difference in dyads was not related to social monitoring (Mantel Z: 232.26, r = 0.13, p = 0.140). During the birth season, rank position for males and females was also unrelated to social monitoring.

Do males monitor differently to females during mating season?

During the mating season, males monitored both female friends: t(11) = 0.013, p = 0.990 and female non-friends: t(11) = -0.488, p = 0.635, at equal rates to the females. Males also monitored male friends: t(7) = -2.236, p = 0.030 and male non-friends: t(11) = -1.988, p = 0.036 at significantly higher rates than females (Figure 3.6). In contrast, during the birth season, males monitored female friends significantly less than females monitored female friends.

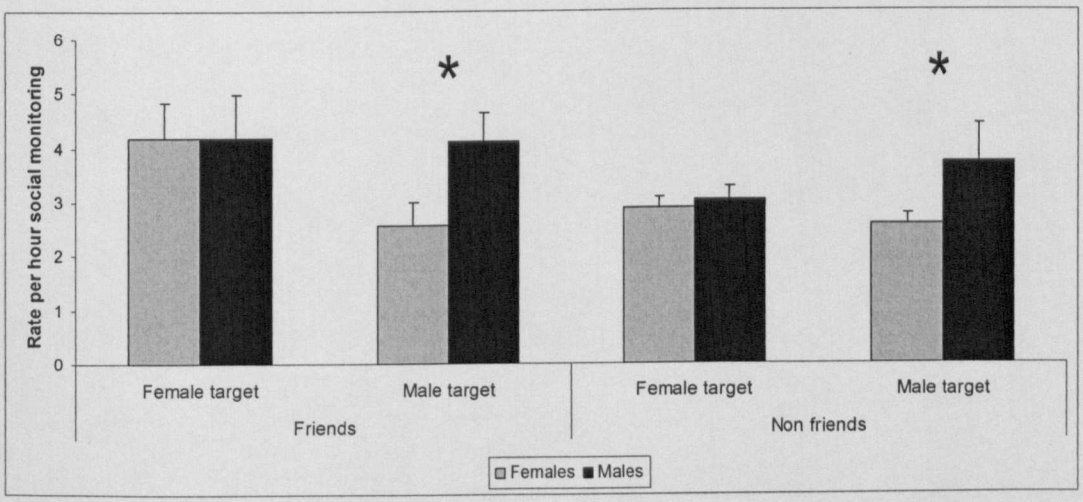

Figure 3.6 Social monitoring of friends and non-friends by male and female ring-tailed lemurs in mating season.

How does the monitoring of friends and non-friends compare between seasons?

Females

During the mating season, females monitored female friends at a rate of four times per hour, and this was a significant hourly decrease in mating season: $t(6) = 2.820$, $p = 0.030$. Females monitored female non-friends: $t(6) = -0.588$, $p = 0.578$ and male friends consistently across seasons: $t(3) = -1.107$, $p = 0.349$. During the mating season, male non-friends were monitored significantly more frequently than the birth season: $t(6) = -8.963$, $p = <0.001$ (Figure 3.7).

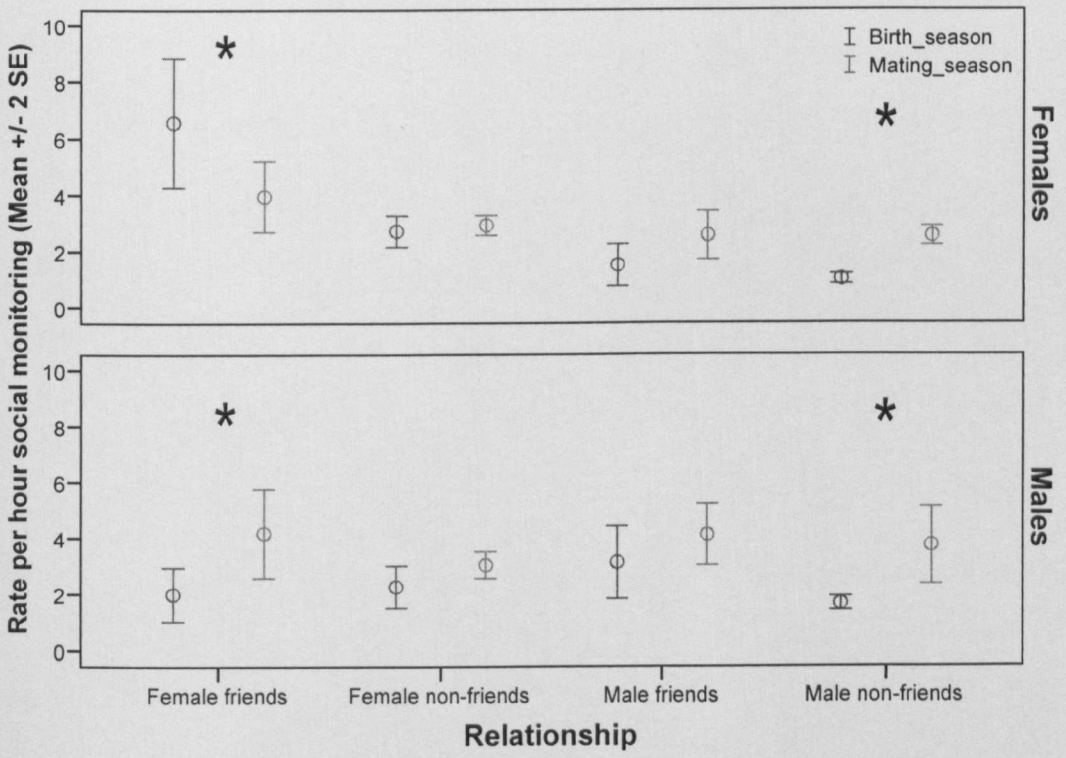

Figure 3.7 Seasonal changes in ring-tailed lemurs' social monitoring

Males

During the mating season, males monitoring increased for all targets (Figure 3.7). Female non-friends were monitored at the lowest rate, roughly three times per hour. During the mating season, male monitoring of female friends significantly increased compared to birth season: $t(9) = -2.437$, $p = 0.038$, as did monitoring of male non-friends: $t(10) = -3.511$, $p = 0.006$. Monitoring of female non-friends: $t(10) = -1.569$, $p = 0.148$ and male friends: $t(9) = -1.016$, $p = 0.336$ remained similar across seasons.

Discussion

Study 2 demonstrates some novel findings concerning social and seasonal influences on visual attention in ring-tailed lemurs. Social monitoring during the mating season was different for males and females, and particularly with respect to the sex composition of the dyad in which they were interacting. Additionally, the results indicate that if social relationships remain stable over seasons, rates of visual monitoring also remain consistent.

How does social monitoring change between seasons?

The behavioural correlates of monitoring

Females. Females have an affiliative basis of social monitoring that persists across seasons. Despite individual friendships changing during the seasons, female-female dyads that engaged in higher levels of social monitoring had a higher sociality index score, did not monitor one another due to agonism or rank differences, and spent roughly the same visual budget monitoring conspecifics across seasons. This is supported by the fact that female-

female social dynamics, e.g. rate of aggression and sociality scores remained relatively similar from birth season to mating season, consistent with Taylor & Sussman's (1985) findings of stability in female-female relationships.

In contrast, most heterosexual relationships formed during the birth season did not persist through to mating season. Female-male agonism was also higher during the mating season, brought on by the male's frequent sexual approaches (Jolly, 1966; Sauther, 1991). However, females' monitoring of males remained correlated with sociality index scores (as in the birth season) and unrelated to agonism in mating season.

Males. During the mating season, changes occur in male sociality and affiliative behaviour (Gould, 1997), agonism (Jolly, 1966; Koyama, 1988; Sauther, 1991), dominance ranks (Jolly, 1966; Parga, 2006; Taylor & Sussman, 1985) and troop membership. This behavioural instability was mirrored in visual attention, with an agonistic influence on males' social monitoring. It seems likely that the high incidence of aggression from all males contributed to increased monitoring, especially as dyads with an antagonistic relationship monitored more frequently than dyads with a higher sociality index score unlike that observed during the birth season.

Like male-male monitoring, male to female social monitoring was unrelated to sociality index scores and positively correlated with agonism during mating season. This is interesting as in both seasons, males did not receive less aggression from female friends, yet in birth season, the basis of monitoring was affiliative rather than agonistic. The increase in aggression

received from females during mating season, may have contributed to this change in the basis of monitoring.

Sex differences in frequencies of social monitoring

During the birth season, females monitored more frequently than males. However, during mating season, males monitored significantly more frequently than females. While reports suggest estrous females engage in increased social monitoring (Keverne et al., 1978) and heightened vigilance (Yamamoto, 2005), the current study indicated little change in the visual budgets of female lemurs during mating season. Keverne et al. (1978) reported high rates of male social monitoring directed towards females rather than males during estrous periods. However, in the present study, male and female lemurs monitored females at an equal rate, while males monitored male targets significantly more often than the females did. Therefore, increased male social monitoring during the mating season appears to be a result of the motivation to monitor male competitors.

Change in targets of social monitoring

Females. Females did not increase monitoring of either male or female friends during the mating season; however, male non-friends were monitored significantly more during the mating season compared to the birth season. There may be several reasons for this: males approached and tail waved at female friends and non-friends during the mating season. However, nearly all observed copulations involved a male non-friend (also reported by Gould, 1996b). Male-female affiliative relationships do not necessarily confer a

mating advantage (Gould, 1996b) and in this study, females did not increase monitoring of male friends between seasons but increased monitoring of male non-friends and mated with them. This increased monitoring of male non-friends/potential mating partners during mating season may reflect female mate choice.

Males. Males monitored female friends significantly more often during the mating season than the birth season. Given that males primarily mated with female non-friends, this finding was unexpected. However, there are several possible explanations. During mating season, males actually received more aggression from female friends than female non-friends, so increased monitoring between seasons could reflect agonistic influences on monitoring rather than mating preferences, as males primarily copulated with female non-friends. Although males approached and tail waved at female friends and female non-friends equally, increased monitoring of female friends during the mating season may have been a male mating strategy of monitoring receptivity (Sauther, 1991). Finally, maintaining affiliative relationships with female friends may have increased access to the central female core, facilitating proximity and potential mating opportunities with other receptive females (Sauther, 1991).

General Discussion

Little research has been conducted on the stability of social monitoring across time or seasons in primates. What we do know so far is that social monitoring changes in response to events such as food competition (Blois-

Heulin & Girona, 1999; Blois-Heulin & Martinez-Cruz, 2005), the presence of estrous females (Keverne et al., 1978; Treves, 1999), predation (Coss, Marks & Ramakrishnan, 2002) and group membership (Jack, 2001). In the study troop, numerous behavioural changes occurred between seasons, and the current study contributes greater knowledge of the variables related to social monitoring, in lemurs and in a free-ranging group.

Further research during the year would confirm if social monitoring among ring-tailed lemurs persists through periods with differing levels of within-troop competition and environmental influences. Male social monitoring is more fluid than that observed in the females, with increased monitoring of all targets during mating season. Some studies have reported that male vigilance is directed towards potential mates and competitors in other groups (Baldellou & Henzi, 1992; Cowlishaw, 1998). However, Gould et al. (1997) suggested that *Lemur catta* vigilance is associated with detection of predators rather than conspecifics. In the current study, vigilance directed outside the troop did not change appreciably between seasons in this free-ranging troop of lemurs.

In contrast to the attention structure theory (Chance, 1967; Chance & Jolly, 1970), social monitoring in this population of lemurs at Berenty does not have a purely agonistic or rank basis. Keeping track of female friends may be important for female lemurs due to their central role in the troop (Jolly, 1966). Given that affiliation and social tolerance are mechanisms that maintain social groups and social bonding (Sussman et al., 2005) particularly in ring-tailed lemurs (Sussman et al., 2003), monitoring conspecifics according to the quality of the relationship may assist with maintaining

cohesion and proximity in free-ranging primates. However, for males, less differentiated relationships (particularly in mating season) and receiving similar levels of agonism from friends and non-friends alike, means that monitoring equally across the troop and in response to increased levels of intra-troop competition may be a more adaptive strategy. This is in line with suggestions that social monitoring varies according to the state of relationships, the level of tension within the group and individual proclivities (Dunbar, 1988).

Directions for future research

Clearly, more research needs to be conducted on visual monitoring and seasonal influences on behaviour, as most studies on *Lemur catta* are conducted during the birth/lactation season. In order to understand how visual attention affects group living and cohesion in primates, vigilance within the group needs to be assessed across all seasons as it may reveal important targets of attention in addition to predators. If visual attention is influenced by season, then estimates of vigilance or scanning effort may be inaccurate if social monitoring is not included and calibrated for season. Additionally, the role of social monitoring depends on the quality of the dyadic relationship. If relationships are stable across seasons, with low rates of agonism in dyads with a good relationship, then social monitoring may also remain consistent, and reflect an affiliative basis rather than agonism. In female-female *Lemur catta*, visual maintenance of affiliative relationships through keeping track of friends may also be important in defending territory (Nakamichi & Koyama, 1997; Nunn & Deaner, 2004) and avoidance of targeted aggression (Pereira & Kappeler, 1997; Vick & Pereira, 1989). In

dyads where social relationships are more ambiguous, e.g. heterosexual dyads, monitoring may reflect avoidance of agonism particularly by the males. If social relationships are seasonally unstable, namely through increased agonism and competition, visual monitoring of conspecifics reflects the instability of group dynamics, evident in male-male dyads. However, during the mating season, monitoring of potential sexual partners may also play a role in shaping patterns of visual attention (Keverne et al., 1978; Treves, 1999).

The analysis of dyads may be a useful way to proceed in assimilating social data with attention data thus taking into account the contribution of both dyad partners and the quality of the social relationship. Long-term studies on *Lemur catta* sociality and vigilance would help resolve some of these outstanding issues.

CHAPTER 4

DYADIC QUALITIES OF SOCIAL MONITORING IN FREE-RANGING CHACMA BABOONS (PAPIO HAMADRYAS URSINUS)

Overview

In this chapter, I examine dyadic social attention in free-ranging baboons. While a great deal of information is known on baboon sociality, the role visual attention plays in maintaining and keeping track of friends in baboons is unknown. Particular reference is made to the application of traditional techniques of measuring primate social behaviour and the utility of using these approaches in social attention. I assess the role of dyadic social relationships in social monitoring and as a function of dyad sex composition. An additional focus of this chapter is on the symmetry of monitoring within baboon dyads and whether it varies as a function of the social relationship between partners.

Introduction

Primates spend considerable time monitoring conspecifics within the same social group (Treves, 2000) and as reviewed in the introduction, frequent visual attention is commonly associated with the level of threat and competition within the social group (e.g. Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998; Pannozzo et al., 2007). However, patterns of social monitoring between species, and within the same social group, are by no means consistent (Emory & Harris, 1981a; Torres de Assumpção & Deag, 1979). Part of the reason for this inconsistency may be attributable to the use of individuals as the unit of analysis. This is usually achieved by summing an individual's frequency of monitoring (across all individuals within the group) and correlating rates of monitoring with their rank position. This method fails to document exactly who an individual may be looking at and why.

Studies that have focused on the dyadic quality of social monitoring, have found less support for rank based social monitoring (Strayer & Gariepy, 1986). It is likely that dyads vary immensely in the amount of attention exchanged between the social partners according to the quality of the social relationship, which has not been explored in detail. For instance, some dyads that possess an agonistic relationship may monitor more frequently than dyads that possess a good relationship (Watts, 1998). But partner A may have both an agonistic and affiliative relationship with partner B. For instance, females may monitor the alpha male frequently, partly because of the risk of aggression (due to male dominance and larger size) and partly because of the close affiliative relationships between some males and females (Dunbar, 1983; Emory, 1976ab; Watts, 1998).

Applying principles from social behaviour to social attention

An additional benefit of studying dyads is that the relative contribution of both partners' visual attention can be compared. The subordinate partner in a dyad may monitor more frequently than the dominant partner in a dyad (McNelis & Boatright-Horowitz, 1998); however, this asymmetry has not been explored further in studies of social monitoring. Visual attention is thought to be asymmetrical in relation to rank relationships at least, perhaps due to the idea that social monitoring is also an index of nervousness (Dunbar, 1988; Mitchell, 1972). At an individual level, dominant animals tend to receive more attention than they give, and the opposite is true for subordinates (Emory & Harris, 1981a; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998; Pannozzo et al., 2007). An additional role of social monitoring, that attention may be used to track friends (Dunbar, 1988), has received little consideration. In this case, when social monitoring is influenced by affiliation, monitoring is more symmetrical between dyad partners (Strayer & Gariepy, 1986).

Complex social relationships = complex social monitoring

Little is known about social attention in savanna baboons. Early descriptive accounts of baboons' vigilance (Altmann, 1980; Hall, 1960) suggest that baboons spend considerable time monitoring the environment. Vigilance in olive baboons is suggested to have both social and anti-predatory functions, and differences exist between males and females (Alberts, 1994). A wealth of data on social behaviour in baboons indicates that baboon society is socially complex (e.g. Cheney & Seyfarth, 2007; Dunbar, 1988; Silk et al.,

1999). The quality of social relationships in baboons ranges from highly antagonistic in male-male dyads (Smuts, 1985), to varying quality in female-female dyads and heterosexual dyads. Intense affiliative relationships are formed between some males and females (Lemasson, Palombit & Jubin, 2008; Palombit, 2000; Palombit, Seyfarth & Cheney, 1997; Smuts, 1985, Strum, 1987; Weingrill, 2000). Female baboons also form strong relationships with other females, often kin (Silk et al., 1999; 2006a; Silk, Alberts & Altmann, 2006b), and this social integration facilitates infant survival (Silk, Alberts & Altmann, 2003).

In sum, both competition and cooperation are important in baboon societies. Visual attention in baboons can be used simultaneously to threaten an individual and recruit support by rapid head movements between the aggressor and supporter (Packer, 1977). Baboons are characterised as social strivers, that is, maintaining old relationships and making new relationships are important for reproductive fitness (Cheney & Seyfarth, 2007; Silk et al., 2003).

Assessing dyadic attention in baboons

The dyadic approach is ideal for studying social monitoring in baboons, as social relationships clearly vary according to sex and characteristics such as kin, rank and age. While the attention structure theory suggests that conspecifics are not monitored equally (Chance, 1967; Chance & Jolly, 1970), the large group size of savanna baboons particularly suggests that social monitoring may be directed towards salient targets in the group. Although the influence of group size on social monitoring is inconclusive

(Treves, 1999), analogies drawn from knowledge of social behaviour in baboons may be useful. When social groups are large, more time is spent grooming and/or grooming a smaller number of partners (Dunbar, 1991). Using this perspective, social monitoring may also be directed to a small number of conspecifics, rather than all group members when group size is large.

Strong affiliative or competitive bonds are not characteristic of all dyads in baboons (e.g. Palombit et al., 1997; Silk et al., 1999; 2006ab; Smuts, 1985). For instance, although males form friendships with females, each male is likely to have a different female friend and even within these preferred relationships, the strength is not identical between all dyads classed as friendly (Smuts, 1985). This logic can be applied to social monitoring, in that social monitoring may increase with the strength of the bond. If this is the case, then dyads classed as friends should have a different pattern of social monitoring than those classed as non-friends. However, the case is more complex when considering non-friends because social monitoring between non-friends could be related to a less affiliative relationship e.g. lower grooming and proximity, or related to a more agonistic relationship e.g. frequent aggression. Watts (1998) reported that female gorillas watched females they possessed a neutral to adversarial relationship with, so social monitoring may occur frequently in dyads that interact socially (either affiliatively or agonistically).

The exchange of attention within a dyad

Information on the symmetry of attention could help inform the basis of social monitoring. A number of primatologists suggest that reciprocity or symmetry is an important component of friendship (Goodall, 1986; Maestripieri, 2000; Silk, 2002). In this case, reciprocity refers simply to the balance of behavioural acts given and received (Silk, 2002). In dyads with a strongly positive bond, grooming and proximity are often symmetrical, that is, both individuals contribute equally in maintaining the social relationship (Hohmann, Gerloff, Tautz & Fruth, 1999; Manson, Rose, Perry and Gros-Lewis, 1999; Silk et al., 1999; 2006b; Watts, 2002).

If social monitoring is indicative of relationship quality, dyads with a good relationship should be characterised by more reciprocal social attention, that is, A monitors B as equally as B monitors A. In contrast, particularly in agonistic or competitive dyads, attention should be more one-sided, that is one dyad partner may contribute more attention than the other dyad partner.

The aim of this study is determine the social basis of dyadic attention in baboons using three measures of relationship quality: sociality/friendship index score (Silk et al., 2006a), agonism, and rank (see chapter 2 for more information on these indices). These measures are expected to vary according to sex composition of the dyad and thus if there are systematic sex influences on social monitoring, then attention will vary as a function of dyad composition.

How dyad composition may influence social monitoring

Male-male dyads

Competition for high rank is a central feature of life history in male baboons (Cheney & Seyfarth, 2007), thus males generally interact in tense and highly competitive ways (Smuts, 1985). Unlike East African baboons, male chacma baboons do not form alliances (Henzi & Barrett, 2003) or interact affiliatively with one another. Therefore, social monitoring in male-male dyads is hypothesised to reflect solely competitive influences that would manifest as rank and/or agonistic influences on attention.

Heterosexual dyads

In contrast, male baboons form both enduring affiliative relationships with some females whilst behaving agonistically towards other females (e.g. Palombit et al., 1997; Smuts, 1985). Therefore, for male-female dyads, social monitoring is predicted to reflect the strength of the affiliative relationship. The benefits of heterosexual friendships for females have been discussed in detail, such as protection against harassment or infanticide (Altmann, 1980; Palombit, 2000; Palombit et al., 1997; Smuts, 1985; Weingrill, 2000). Females may also receive lower levels of agonism from a male friend compared to a non-friend (Lemasson et al., 2008).

Consequently, female baboons may invest more heavily in a heterosexual friendship than males do (Palombit et al., 1997; Smuts, 1985). Therefore, within a heterosexual dyad, the symmetry of attention may work in one of two ways. If asymmetry of attention between dyad partners is associated with agonism, then the female partner would engage in more

frequent monitoring of the male partner than *vice versa*. Accordingly, friendly dyads would be expected to have more symmetrical attention exchanged between partners. Alternatively, if females compared to males invest more heavily in heterosexual friendships, then in all cases, the female dyad partner may monitor the male partner more frequently than *vice versa*.

Female-female dyads

Female-female relationships are hypothesised to reflect affiliative tendencies rather than agonistic influences. The overall social preference of female chacma baboons is for other females (Henzi, Lycett, Weingrill & Piper, 2000; Silk et al., 1999). Females develop highly differentiated social relationships, showing particular affinities for kin, reciprocating partners and adjacently ranked individuals (Silk et al., 1999; 2006ab). Therefore, if social monitoring mirrors social behaviour, three predictions can be made. Dyads that score highly in sociality index scores are expected to engage higher rates of monitoring. Secondly, dyads with a low rank difference may engage in greater frequencies of monitoring. Thirdly, the symmetry of attention within a female-female dyad is expected to vary with the social bond: the friendlier a dyad, the more symmetrical the exchange of attention.

Methods

Study site

The study was conducted at Lajuma Mountain retreat, situated in the Southpansberg mountains, Limpopo, South Africa. The 430ha reserve (elevation 1,290 metres) contained several basic vegetation types, such as

forest, woodland, thicket, grassland (Edwards, 1983) with vegetation characterised by *Acacia karoo, Acacia ataxacantha, Ficus spp., Syzygium cordatum and Zipiphus mucronata.* The baboons' core range encompassed roughly a 15km² area of the reserve. Potential predators of baboons at the site included leopards and brown hyena. Some species of eagles (African crowned eagle and Verreaux eagle) may have posed a predation risk to small baboons (Cheney et al., 2004; Cowlishaw, 1994).

Study species and subjects

Adult members (n = 30) of House troop baboons were studied during February to June 2007. The troop had not been studied for some time prior to my study, so time was taken to complete a full census of the troop, and to re-habituate the troop to being closely followed again. The troop numbered 61 individuals, and consisted of 10 adult males, 20 adult females, and the remainder were immature baboons. All adult and subadults were individually recognisable, and although immatures did not serve as focal animals, they often featured as interactants.

Data collection and analysis

Data collection protocols and general analyses are listed in chapter 2. Mantel tests were performed separately for male-male, male-female and female-female dyads. These analyses were used to test the relation between: a) social monitoring and agonism; b) social monitoring and affiliation (sociality index scores); and c) social monitoring and rank difference scores. The sociality index was not calculated for male-male dyads. Males did not groom

other males, thus precluding the use of the index. While proximity alone could have been used to assess male-male relationships, high male-male proximity scores in baboons are usually a by-product of frequent proximity to the same female group members (Noe & Sluijter, 1995).

Further correlational analyses were used to compare the influence of the above mentioned social variables on attention between dyads classed as friends compared to those classed as non-friends. Symmetry of monitoring within dyads was assessed using the intra-class correlation for dyads that consisted of same sex individuals (Kenny et al., 2006). This technique is appropriate when the dyad partners are indistinguishable, i.e. the same sex. Intra-class correlations for dyads were interpreted in the same fashion as Pearson's correlations. Thus if a dyad partner had a high score and the intra-class correlation was positive, then the other dyad partner also had a relatively high score. As heterosexual dyad partners were distinguishable on the basis of sex, Pearson's correlations were used to assess the symmetry of attention in line with recommendations from Kenny et al. (2006).

Results

Visual attention budgets

Baboons spent approximately 17% of their visual budget monitoring conspecifics within the group. Males engaged in significantly more social monitoring (19% of visual time) than females did (16% of visual time): $t(28) = -4.773$, $p = <0.001$.

Male-male dyads

Social relationships

As observed in other populations of baboons, male-male relationships were generally competitive and hostile. Agonism occurred in 87% of male-male dyads, and males were involved in significantly more agonistic interactions with other males than with females: $t(9) = -4.208$, $p = 0.002$. On average, male-male agonism occurred 0.30 times per hour.

Social monitoring

The average rate of monitoring within a male-male dyad occurred 1.77 times per hour. Social monitoring was significantly associated with the rate of agonism within male-male dyads (Mantel Z: 51.378, $r = 0.27$, $p = 0.031$). This indicated that dyads that had an increasingly antagonistic relationship tended to monitor more frequently than dyads with a less hostile relationship (Figure 4.1). However, monitoring was not associated with rank differences between males (Mantel Z: 159.37, $r = -0.22$, $p = 0.935$). That is, dyads closer in rank position did not monitor differently from dyads with more disparate rank positions.

Symmetry of attention with the dyad

Within a male-male dyad, the intra-class correlation for male-male monitoring was non-significant: $r = 0.14$, $F(44,44) = 0.750$, $p = 0.828$. This indicated that monitoring between male dyad partners was exchanged unequally between partner A compared to partner B (Figure 4.2a)

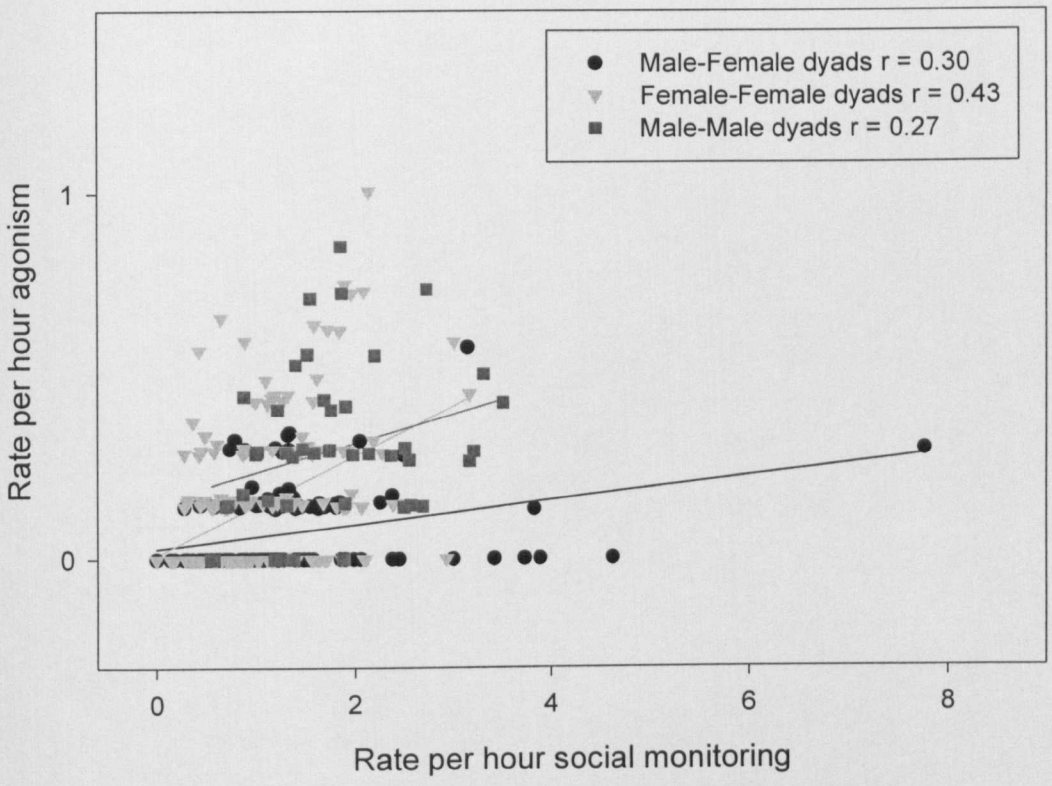

Figure 4.1 The relation between agonism and social monitoring in baboons.

Heterosexual dyads

Social relationships

Almost all the females formed friendships with certain males. The median value of the sociality index score for heterosexual dyads was 0.37, indicating that most bonds between male and female baboons were weak. Females were as likely to receive aggression from a male as they were from a female: $t(19) = -1.360$, $p = 0.190$. Within a heterosexual dyad, agonism occurred at a relatively low rate of 0.07 times per hour.

Social monitoring

The average rate of heterosexual dyadic monitoring was 1.15 times per hour. The sociality index score was positively associated with social monitoring by males towards females (Mantel Zr: 3389.1, r = 0.78, p = 0.001) and by females towards males (Mantel Zr: 2303.0, r = 0.78, p = 0.002). Agonism was also positively correlated, to a lesser extent, with social monitoring from males to females (Mantel Zr: 62.75, r = 0.30, p = 0.002) and females towards males (Mantel Zr: 39.93, r = 0.29, p = 0.003).

The influence of aggression and sociality scores on monitoring were considered separately for dyads classed as friends (by scoring above the 95% confidence interval of the sociality index mean) compared to non-friend dyads. In friendly heterosexual dyads there was no influence of agonism on sociality scores: (n = 26), r = 0.15, p = 0.453, and no influence of aggression on attention: (n = 26), r = 0.27, p = 0.176. However, for male-female non-friends, there was a correlation of sociality with agonism: the higher the sociality index score, the higher the rate of agonism: (n = 124), r = 0.17, p = 0.031. Thus, a positive relation was found between agonism and social monitoring in non-friend heterosexual dyads: (n = 124), r = 0.35, p = <0.001.

Symmetry of attention within a dyad

The symmetry of social monitoring in heterosexual dyads was analysed by comparing the female partner's rate of monitoring to that of the male partner. Because symmetry may be related to the strength of the affiliative relationship, dyads classed as friends were considered separately from non-friend dyads (Figure 4.2b).

For male-female friends, a positive Pearson's correlation between rates of attention from the female partner and the male partner indicated that if a male's attention towards the female partner was high, the female's attention to the male was also high: (n = 26), r = 0.62, p = 0.001. In dyads classed as non-friends, there was no symmetry of social monitoring: (n = 124), r = -0.04, p = 0.621.

Female-female dyads

Social relationships

Females formed friendships with other females as evidenced by close proximity and frequencies of grooming. However, social bonds in most female-female dyads were weak, with a median value of 0.40 on the sociality index.

Social monitoring

In female-female dyads, social monitoring occurred at a rate of 0.96 per dyad. Like heterosexual dyads, social monitoring was related to both the sociality index score (Mantel Z: 507.00, r = 0.35, p = <0.001) and the rate of dyadic agonism (Mantel Z: 73.209, r = 0.43, p = <0.001). However, in female-female dyads, rank difference was related to the frequency of social monitoring (Mantel Z: 2347.2, r = -0.18, p = 0.010). Specifically, dyads closer in rank tended to engage in more frequent monitoring compared to dyads with a larger rank difference.

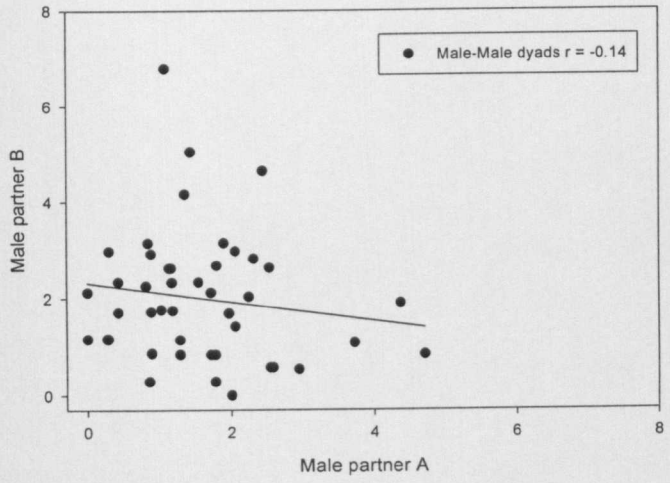

Figure 4.2a

Male-male dyads

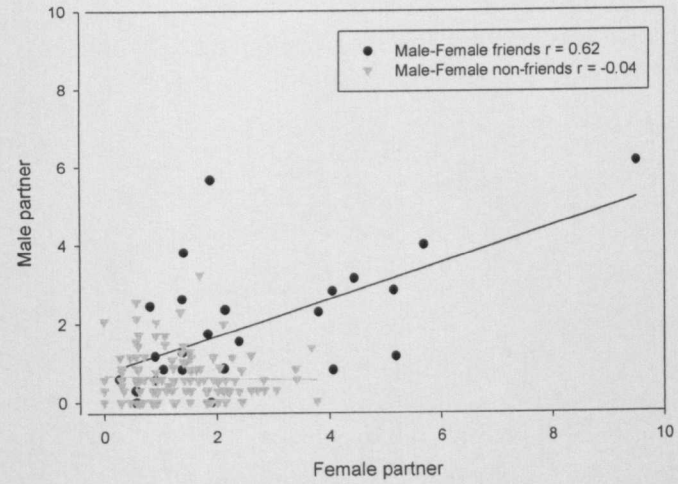

Figure 4.2b

Heterosexual dyads

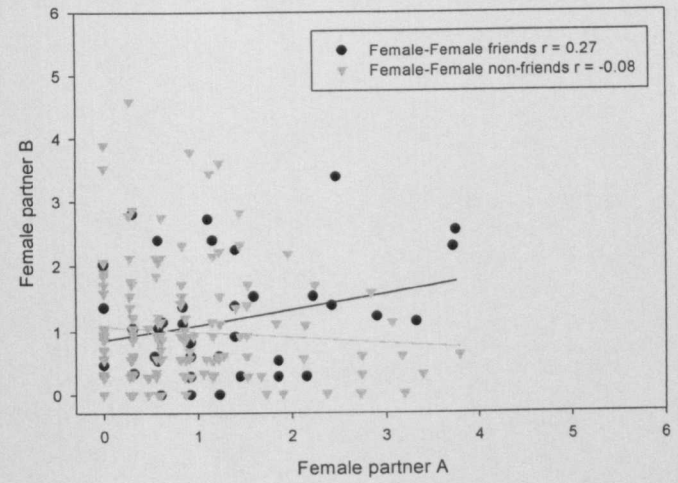

Figure 4.2c

Female-female dyads

Figure 4.2 The symmetry of attention within baboon dyads.

When friends were compared to non-friends, there was no relation between agonism and the strength of the affiliative relationship (as measured by the sociality index score) for female-female friend dyads: (n = 40), r = -0.05, p = 0.773. Even in friendly dyads, attention increased in line with the rate of agonism: (n = 40), r = 0.46, p = 0.003. In female-female non-friend dyads, there was a significant relation between sociality and agonism: (n = 150), r = 0.31, p = <0.001. The higher the sociality index score (but not high enough to be classed as friends), the higher the agonism. Additionally, in non-friend dyads, social monitoring was related to agonism: (n = 150), r = 0.36, = <0.001.

Symmetry of attention within a dyad

In terms of symmetry of monitoring (assessed by the intra-class correlation), females in friendly dyads monitored each other equally: r = -0.27, F(39,39) = 1.721, p = 0.047 whereas females in non-friend dyads monitored asymmetrically: r = -0.08, F(149,149) = 0.852, p = 0.835, Figure 4.2c.

Discussion

The influence of relationship quality on social monitoring

Overall, both agonistic and affiliative tendencies influenced social monitoring in this population of free-ranging baboons. In line with predictions, male-male monitoring was influenced by the frequency of aggression, but not rank difference. Although baboon males form a linear, transitive hierarchy, rank is not stable over time (Cheney & Seyfarth, 2007). Frequent rank reversals in the outcome of dyadic agonistic encounters have been reported among male

baboons (Smuts, 1985). Therefore, if male rank was unstable, rather than attention being given to high-ranking males in the current study, attention was directed particularly to males with whom a male had an increasingly antagonistic relationship.

However, not all visual monitoring by male baboons was agonistic. All males formed close relationships with at least one female, and more social monitoring occurred within these friendly dyads. Yet the picture of social monitoring is more complicated than previously anticipated with clear independent effects of agonism on relationship quality and consequently social monitoring. For instance, in heterosexual friends, agonism did not influence social monitoring, whereas, in non-friend dyads it did. When the troop as a whole was considered, agonism was positively correlated with monitoring; however, the majority of dyads in the matrix analysis were non-friends (only 15% of heterosexual dyads were classed as friends). Accordingly, it was appropriate to consider friend and non-friend dyads separately to elucidate the effects of friendship and agonism on monitoring.

Friendly male-female dyads showed two main qualities not evident in dyads with a less bonded relationship: symmetry of attention and a lack of agonistic influences on monitoring. In heterosexual dyads that were categorised as non-friends, the female partner monitored more frequently than the male partner, whereas in friendly dyads, monitoring was more equal between the partners. Similarly, in dyads with a good relationship, there was no influence of agonism, whereas in non-friends, attention rose in line with agonism. These results supported predictions because dyads whose monitoring was influenced by agonism, also monitored asymmetrically.

Although females invest heavily in heterosexual relationships (Palombit et al., 1997; Smuts, 1985), in the current study, females contributed more attention compared to the male partner only in non-friend dyads.

Female-female dyads showed similar trends to the heterosexual dyads; however, females closer in rank tended to monitor more frequently. Additionally unlike in heterosexual dyads, even social monitoring in friendly female-female dyads was influenced by agonism. This is at odds with the finding of symmetry of attention within female-female friend dyads. Within a dyad, attention may be directed to others both to aggress an individual, and in response to agonism. There is little evidence supporting the role of social monitoring in order to target individuals to aggress (studies generally focus on aggression received), but this may be the case for female-female dyads. Alternatively, female baboons close in rank tend to be related (Cheney & Seyfarth, 2007; Silk et al., 1999; 2006ab) and agonism higher in kin dyads (Bernstein, 1991). Hence, symmetry of attention may be related to both kin relationships and agonism. There was no data available on kin relationships for the study troop. However, whether the females were related or not, social monitoring occurred at a greater rate in closely ranked dyads that possessed both an affiliative and agonistic relationship.

Why do baboons have both an affiliative and an agonistic basis of monitoring?

The baboon results may be strongly related to proximity and spatial association patterns. In larger baboon groups, individuals tend to form subgroups whilst foraging or resting (Cheney and Seyfarth, 2007; Smuts,

1985). Therefore, all social interactions, both agonistic and affiliative, could occur within subgroups rather than between individuals from different subgroups as the frequency of aggression can be a direct function of the amount of time spent in proximity (Bernstein, 1991; Smuts, 1985). In the current study, aggression rates were similar regardless of the relationship quality for both heterosexual and female dyads, so friends were not benefiting from reduced aggression as reported by Smuts (1985) for heterosexual friendships (but see Lemasson et al., 2008). In macaques, females are more likely to groom higher-ranking females who threaten them at high rates, suggesting that grooming by high-ranking females may be used as a form of extortion (Silk, 1982). When aggression is low, grooming between high- and low-ranking baboon females becomes more symmetrical, as low-ranking females are less likely to exchange grooming for tolerance (Barrett, Gaynor & Henzi, 2002).

Is aggression indicative of a poor relationship? It appears not if affiliative interactions are considered in parallel. For instance, in baboon males, competition and aggression are important for achieving status within the troop (Noe & Sluijter, 1995). In heterosexual and female-female baboon dyads, high agonism and low affiliation/proximity illustrated a weak relationship, while low aggression and high affiliation characterised a good relationship. However, social monitoring does not appear to fit these neat categories. Attention may also be bimodal: high levels of attention to friends and to adversaries with low levels of attention to individuals somewhere in the middle, i.e. neutral relationships. Differentiation of friendly dyads vs. neutral dyads vs. adversarial dyads would help address this issue.

The significance of symmetry of monitoring in baboon dyads

Symmetry or reciprocity of social interactions, particularly grooming (Silk et al., 1999; 2006b) and proximity (Palombit et al., 1997; Smuts, 1985), are important when considering the strength of the social bonds. The stronger the social bond, the more equal the contribution, e.g. grooming equity between dyad partners (Silk et al., 2006b). In traditional accounts of the structure of social attention (Chance, 1967; Chance & Jolly, 1970), social monitoring is perceived as relatively one-sided. At the individual level, high-ranking animals may receive more attention than they give (Keverne et al., 1978; Pannozzo et al., 2007). Within a dyad, the lower-ranking individual may look at the higher-ranking individual more frequently and this attention is not reciprocated by the higher-ranking individual (McNelis & Boatright-Horowitz, 1998). However, because neither social monitoring nor the relationship quality between dyads has been systematically tested, there are few data examining the patterning of social monitoring among conspecifics and why it may be higher in some dyads compared to others.

A new approach to social monitoring

This study provides support for the benefits of assessing social attention at the dyadic level. The distribution of social monitoring is not equal within a group, and furthermore social monitoring may not be equal between dyads or within dyad partners. Heterosexual and female-female dyads' monitoring is influenced both by affiliative and agonistic influences and this may be because friendships do not necessarily confer a reduction in agonism. If this is the case, how can the underlying basis of monitoring in baboons be

clarified? Whether attention between dyad partners is distributed symmetrically seems like a good starting point. Given that strong social bonds in baboons are characterised by more equity in affiliative behaviour (Silk et al., 1999; 2006b), it is possible that social monitoring may also function similarly. Indeed, in this study friendships were characterised by more symmetrical attention patterns, suggesting both dyad partners were investing similar amounts of visual time in monitoring one another.

A final issue concerns the benefits that may be gained from maintaining visual contact with a friendly conspecific. Both male and female baboons benefit from forming friendships. Females benefit from friendships with males in terms of protection against harassment from conspecifics, protection of infants from predators and other baboons, and increased foraging efficiency (Altmann, 1980; Smuts, 1985). Recent evidence (particularly pertaining to chacma baboons) suggests that heterosexual friendships protect a female and her offspring against infanticidal males (Palombit et al., 1997; Palombit, 2000; 2006). Heterosexual friendships may facilitate a male's evaluation of mating opportunities, use of infants as buffers against agonism, integration into the troop and protection of offspring if the male is a sire of a female friend's infant (Smuts, 1985; Strum, 1987; Weingrill, 2000).

Female-female friendships are also beneficial. Female baboons that are more socially integrated with other females have greater reproductive success (Silk et al., 2003). Females are more anxious when they are isolated from group members (Castles, Whiten & Aureli, 1999) so friendships might have direct psycho-emotional benefits. Taken together, social monitoring in

affiliative dyads may be important for maintaining proximity (Rowell & Olson, 1983), initiating affiliative behaviours (Strayer & Gariepy, 1986) and monitoring allies (Dunbar, 1983) given the potential benefits of friendship for both individuals.

Information on visual attention in baboons is lacking. Social factors influence baboon vigilance (Alberts, 1994) and factors such as maternal style rather than dominance rank, influence the propensity to which baboon mothers visually attend to conspecifics (Altmann, 1980). While baboons in large groups tend to be more vigilant, this is attributed to predation risk rather than conspecifics (Cowlishaw, 1998; Hill & Cowlishaw, 2002). Despite the social complexity evident in baboon societies, there is little information on whether social monitoring in baboons is also used in a multi-faceted way. This chapter takes a first step towards assessing social influences on visual attention in baboons. More long-term data with respect to social relationships would help ascertain why monitoring in particular dyads frequently occurs, and what purpose this monitoring serves.

This chapter indicates that assessing dyadic social monitoring is a useful way to consider attention, especially in terms of the patterning, frequency and symmetry between dyad partners. Importantly, the frequency of social monitoring varies according to the relationship between individuals and the sex composition of dyads. In this sense, consideration of both the target and the relationship appears particularly important for documenting proximate mechanisms of visual attention within primate groups.

CHAPTER 5

ATTENTION STRUCTURE IN CAPTIVE CHIMPANZEES, ORANG-UTANS AND SIAMANGS

Overview

I use a comparative approach in this chapter to evaluate social monitoring in three species of captive apes with reference to the attention structure theory (Chance, 1967; Chance & Jolly, 1970). Several hypotheses generated by the theory are tested, based on the theory's emphasis of social attention in centripetal (rank) species compared to acentric (absence of rank) species. I also test alternative hypotheses based on social relationships within species, to examine the social behavioural correlates of visual attention in captive apes. If attention structure differs among species, the strength of social relationships within the species, rather than the presence or absence of a dominance hierarchy, may account for species-level variation in social monitoring.

Dissemination of research from this chapter

Lane & Bard (2006). Visual monitoring in captive chimpanzees, siamangs and orang-utans. Poster presentation at the International Society of Primatologists meeting, June 25-30, Entebbe, Uganda.

Introduction

The motivation to monitor conspecifics within primate groups is usually considered as an attribute of an individual and as an attribute of social organisation. For instance, individuals that receive more aggression (Keverne et al., 1978; Pannozzo et al., 2007) or are low status (Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998; Pannozzo et al., 2007) may engage in frequent social monitoring. The propensity to monitor conspecifics is also considered as a function of social organisation (Caine & Marra, 1988); this chapter focuses on a comparative approach to social monitoring.

Acentric and centric social organisation

The attention structure theory (Chance, 1967; Chance & Jolly, 1970) suggested that social attention in primates was indicative of social organisation, and particularly the rigidity of the dominance hierarchy within a group. Chance and other authors argued that social organisation could be classified along a continuum of centripetality and acentricity, which social attention also followed (Chance, 1967; Chance & Jolly, 1970, Emory, 1976ab; Emory & Harris, 1981ab). For instance, species characterised as acentrically organised lack group coherence, have weak or no rank relationships and consequently attention is directed outwardly towards the environment rather than conspecifics. In contrast, centripetal societies are organised and cohered by rank relationships, hence attention is directed inwardly towards conspecifics, particularly to monitor dominant animals (Chance & Jolly, 1970, Emory, 1976ab; Emory & Harris, 1981ab). Accordingly, dominant individuals in centripetal groups receive the most

attention, and subordinates engage in frequent social monitoring of dominant individuals. This may be because dominant conspecifics engage in 'attention getting behaviours' such as displays (Chance & Jolly, 1970; Reynolds & Luscombe, 1969; 1976) and subordinates must monitor the position and location of dominant individuals to avoid aggression (Chance & Jolly, 1970).

Apportioning attention to social and non-social targets

Social organisation influences the distribution of social attention vs. non-social attention in squirrel and tamarin monkeys (Caine & Marra, 1988). Tamarin monkeys (a species characterised by the absence of rank relationships and presence of cooperative relationships) engage in more non-social than social monitoring compared to hierarchically organised and more aggressive squirrel monkeys (Caine & Marra, 1988). Treves and Baguma (2002) reported that females in egalitarian species of primates engaged in less frequent monitoring than despotic species. However, in both these studies, species differences in social monitoring are only apparent in a feeding context. It is unclear whether social organisation generates differences in social monitoring across all contexts.

However, several questions remain unanswered: a) what factors influence attention structure in primate species with no rank order? While social monitoring may occur at a lower rate in co-dominant species (Caine & Marra, 1988), there is less information on the social targets of monitoring when it does occur. b) How do social relationships, both within species and between species, influence monitoring? Current knowledge suggests that egalitarian groups and/or the absence of rank order may reduce the

propensity to monitor conspecifics (Caine & Marra, 1988; Treves & Baguma, 2002). However, unresolved rank relationships in female gorillas may actually facilitate the monitoring of conspecifics as aggression is bi-directional (Watts, 1998).

How social organisation may influence attention structure

The goal of this chapter is to identify attention structure in three species of apes with contrasting social organisations: chimpanzees, orang-utans and siamangs. As described in chapter 1, information on social monitoring in apes is largely unknown. The distinct social organisations of chimpanzees, orang-utans and siamangs suggest that attention structure and the behavioural correlates of social monitoring may be different in these three species of primates. These differences are likely to be a result of the social bonds within the group, rather than the presence or absence of rank order.

Chimpanzees

Chimpanzee society is characterised by a high level of interindividual tolerance (Boesch & Boesch-Achermann, 2000; de Waal, 1982); however, relationships can be characterised by intense competition (Nishida & Hiraiwa-Hasegawa, 1987). Choice of partners with whom to associate is a fundamental tactic in the social strategies of chimpanzees (Newton-Fisher, 1999). Chimpanzee social relationships are strongest between males, while female-female social relationships are generally weak (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Stumpf, 2007) although this may vary by geographical location (Boesch & Boesch-Achermann, 2000). While males

possess a linear dominance hierarchy, rank relationships vary in females (Nishida, 1979; Wittig & Boesch, 2003).

The fission-fusion social organisation of wild chimpanzees (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Stumpf, 2007) may make social monitoring difficult due to fluid sub-group composition (Mitani, Watts & Muller, 2002a). While social monitoring has not been studied in chimpanzees, social factors are suggested to influence chimpanzee vigilance (Kutsukake, 2006; 2007; Treves, 1997). Kutsukake (2006) reported that chimpanzee vigilance increased when the number of neighbours increased, particularly when non-affiliates were in proximity. Rank does not appear to influence chimpanzee vigilance (Bethell, Vick & Bard, 2007; Kutsukake, 2006). However, Chance (Chance, 1967; Chance & Jolly, 1970) emphasised a rank based and centripetal attention structure in chimpanzees: more attention directed towards conspecifics than to non-social targets, and directed up the hierarchy.

Orang-utans

Orang-utans are characterised as semi-solitary (Galdikas, 1984; McKinnon, 1971; 1974) but they sometimes associate in parties for social benefits (Delgado & van Schaik, 2000). For orang-utans, active avoidance of conspecifics is an important social behaviour (van Schaik, 2004).

Social relationships among orang-utans are generally weak to hostile (van Schaik & van Hooff, 1996), although some females may associate together (Galdikas, 1984). A linear dominance hierarchy is not evident in

female orang-utans (Galdikas, 1984); however, some females may show dominance relationships in captivity (Maple, 1980).

Because of orang-utans' large size, arboreality and reduced risk of predation, orang-utans are not highly vigilant (Setiawan, Knott & Budhi, 1996). Despite the semi-solitary nature of orang-utans, rehabilitant and captive orang-utans visually monitor conspecifics, this decreasing with age (Kaplan & Rogers, 2000; 2002). Orang-utans are considered as an acentric species (Chance, 1976) indicating that attention in orang-utans would be directed towards the environment rather than conspecifics.

Siamangs

Siamangs live in monogamous pairs, with group membership consisting of an adult pair and offspring (Chivers, 1972; 1974; Gittins & Raemakers, 1980; Palombit, 1996). Social bonds and cohesiveness in the siamang are strong: individuals are frequently within 10m of one another throughout the day (Chivers, 1974) and often in non-grooming physical contact (Palombit, 1996). Adult siamangs are usually co-dominant (Gittins & Raemakers, 1980; Orgeldinger, 1991; Palombit, 1996) and aggression in wild siamangs is infrequent (Chivers, 1972; Palombit, 1996), but used to peripheralise maturing offspring (Chivers, 1972).

Despite reports of low predation risk in wild populations of Hylobatidae (e.g. van Schaik, 1983), gibbons spend a high percent of time vigilant (Uhde & Sommer, 2002) and heightened territorial non-social vigilance (directed outside the exhibit) occurs in captive siamangs (Orgeldinger, 1997). Chivers (1972) reported that siamang conspecifics constantly watched one another

and the forest about them, which served to maintain group cohesion and synchronise behaviour. Chance & Jolly (1970) suggested gibbons were acentrically organised, with attention directed outside the group rather than inwardly.

Predicting attention structure in apes

The attention structure theory (Chance, 1967; Chance & Jolly, 1970) generates clear hypotheses about the influence of social organisation on attention structure. The attention structure theory would predict that:

a) Social monitoring should occur more frequently among chimpanzees compared to siamangs and orang-utans given chimpanzees' rank based social organisation.

b) Non-social monitoring should occur relatively more frequently in siamangs and orang-utans compared to chimpanzees.

c) Subordinate chimpanzees should monitor conspecifics more frequently than dominant chimpanzees.

However, these hypotheses based on the attention structure theory do not fully account for social monitoring in species without a dominance hierarchy. Additionally the theory does not take into account the predominantly affiliative nature of most primate groups (Sussman et al., 2005) and that competitive and agonistic influences are not always predictive of social monitoring (Strayer & Gariepy, 1986; Torres de Assumpção & Deag, 1979). An alternative set of hypotheses for social monitoring that take into account the social organisation and within-group relationships of chimpanzees, orang-utans and siamangs are suggested below.

Social monitoring between species

a) Chimpanzees and siamangs monitor conspecifics at equal rates, because keeping track of conspecifics is likely to be important for both species. This is because siamangs and chimpanzees may use social monitoring to maintain cohesion, initiate affiliative behaviours and keep track of salient individuals within the group. Orang-utans monitor conspecifics less frequently than chimpanzees and siamangs because they are less gregarious (summarised in Sussman et al., 2005) and have a semi-solitary social organisation.

b) Species differences in social monitoring occur as a function of the social relationships within the group rather than absence of rank order. If social relationships are strong (chimpanzees and siamangs) compared to weak (orang-utans), social monitoring will occur more frequently.

Social monitoring within species

These predictions focus on the within-group relationships in chimpanzees, siamangs and orang-utans and how they may influence social attention.

a) Chimpanzee social monitoring reflects affiliative relationships. Dyads that have a good relationship are predicted to engage in higher rates of social monitoring than dyads with a weaker relationship. Rank and agonism are not expected to influence social monitoring in chimpanzees. Even though within-group competition can be high in chimpanzees due to the presence of multiple males, more attention is predicted to be directed towards affiliates than adversaries.

b) Siamang social monitoring primarily reflects affiliative influences. Even though siamang relationships are affiliative, dyads that have the most affiliative relationship are predicted to engage in the highest rates of monitoring. Agonism is not predicted to be related to social monitoring in siamangs, as interactions are predominately peaceful (Chivers, 1972; Palombit, 1996).

c) Orang-utan social monitoring reflects agonistic influences. Orang-utans rarely engage in affiliative behaviours and most orang-utan dyads are characterised by weak to hostile social relationships (van Schaik & van Hooff, 1996). Orang-utans may show patterns of social monitoring similar to female gorillas, in that frequent monitoring occurs in non-friendly dyads to avoid one another and because dominance is unresolved and aggression bi-directional (Watts, 1998).

Methods

Study species and housing

Chimpanzees (Pan troglodytes)

Six adult chimpanzees (two females and four males) housed at Whipsnade Zoological gardens, Bedfordshire, UK, were studied. Chimpanzees ranged in age from 9 to 41 years and lived together in a large exhibit consisting of an indoor area furnished with vertical structures and hammocks with access to a large naturalistic outdoor exhibit enclosed by a moat (during inclement weather the outdoor access was restricted). Data on the chimpanzees were collected over a period of 18-months (excluding winter periods).

Orang-utans (Pongo pygmaeus & Pongo abelii)

Nine orang-utans aged from 2.5 to 35 years kept at Zoo Atlanta, Georgia, USA, were studied. Six groups of orang-utans were observed (a total of 15 dyads); however, membership of groups changed between the study periods according to Zoo protocol and medical procedures.

Table 5.1 Orang-utan subjects and groupings.

Group	Group composition	Orang-utans	Study period
Sulango-Miri	1 male, 1 female, 1 infant	Sulango, Miri, Satu*	1 and 2
Allen-Hati	1 male, 1 female	Allen, Hati	1
Allen-Biji	1 male, 1 female	Allen, Biji	2
JT	1 male, 2 females, 1 juvenile male	JT, Daisy, Madu, JR	1 PM only
Female 1	2 females, 1 juvenile male	Biji, Madu, JR	1 AM only
Female 2	2 females, 1 juvenile male	Daisy, Madu, JR	2

* Infant data excluded as non-independent from mother

All orang-utans resided in large naturalistic outdoor enclosures with vertical structures, hammocks and swings. See Table 5.1 for details on groupings. Data on the orang-utans were collected during two intensive study visits, lasting roughly one month each.

Siamangs (Symphalangus syndactylus)

A family group of four siamangs (one adult female, one adult male, two subadult males) aged 5 to 11 years old were studied. They were housed at Marwell Zoological gardens, Winchester, UK and resided in a long indoor-outdoor enclosure, with vertical structures but limited horizontal space. Data

on the siamangs were collected over a period of 14 months (excluding winter periods).

Data collection and analysis

The dyadic association index (Cairns & Schwager, 1987) was used to calculate relationship quality for each species (see chapter 2 for calculation of this index). The chimpanzees had relative rank position (from one indicating the alpha male, to six indicating the lowest ranking in the group) calculated due to the presence of a linear hierarchy. The rank difference between dyad members was also calculated.

Pearson's correlations and Mantel tests were used to assess the relation between dyadic association index scores, agonism and rank difference, with social monitoring. Analyses of variance and *a priori* contrasts were used to analyse individual rates of behaviour, and compare species on social and non-social monitoring.

Results

Comparing between species

Non-social monitoring

There were no differences between the species on frequencies of non-social monitoring: $F(2,23) = 0.661$, $p = 0.526$.

Social monitoring

There was a significant difference in rates of social monitoring among the three species: $F(2,23) = 26.116$, $p = <0.001$. Chimpanzees and siamangs engaged in the highest rates of social monitoring, roughly 35.3 times per hour for the chimpanzees and 43.6 times per hour for the siamangs, although this difference was not significant: $t(23) = -1.535$, $p = 0.138$. The orang-utans engaged in the lowest levels of social monitoring, roughly 15 times per hour, significantly lower than the chimpanzees: $t(23) = 5.119$, $p <0.001$ and siamangs: $t(23) = -6.156$, $p = <0.001$.

Social monitoring within dyads. Social monitoring was also considered at the dyadic level according to species. This analysis asked whether the rate of monitoring between any two individuals in the group differed by species (Figure 5.1). Within a siamang dyad, monitoring on average occurred 14 times per hour. Chimpanzee and orang-utan dyads monitored approximately 7 times (chimpanzees) and 9 times per hour (orang-utans).

The greatest variability in social monitoring was evident in orang-utan dyads. Some orang-utan dyads engaged in low levels of social monitoring, while in other dyads, social monitoring occurred frequently. However, there were no significant differences between monitoring in dyads as a function of species: $F(2,23) = 2.576$, $p = 0.098$.

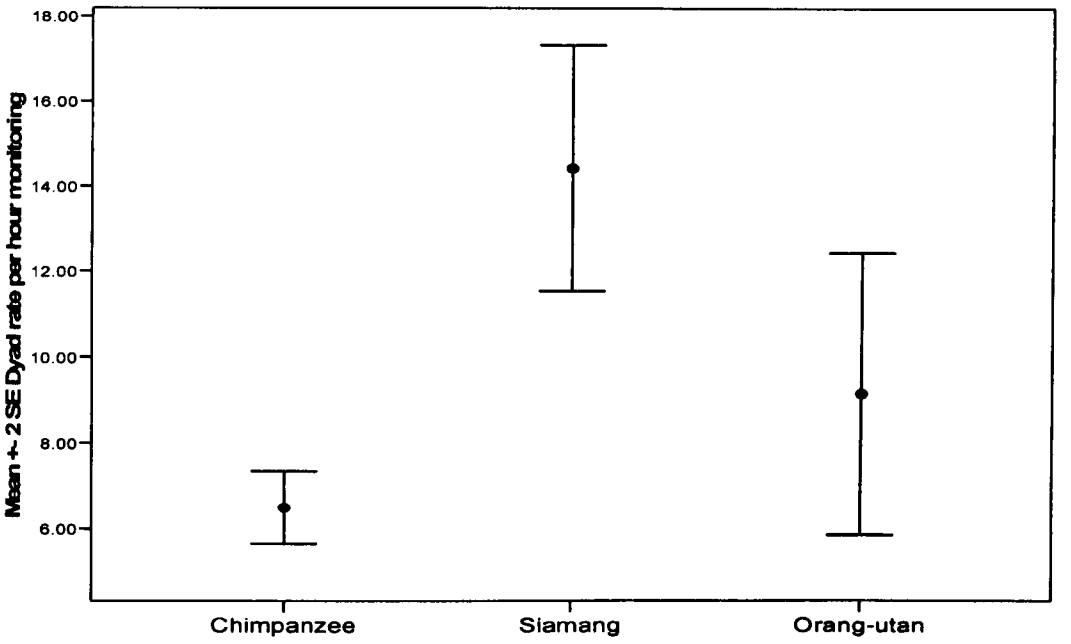

Figure 5.1 Mean rate of social monitoring occurring within chimpanzee, siamang and orang-utan dyads.

Does group size account for the variability of orang-utan social monitoring? Orang-utan social monitoring varied as a function of group size: $F(2,13) = 4.726$, $p = 0.029$. Groups consisting of three individuals, monitored at similar rates to pair-housed orang-utans: $t(13) = -0.685$, $p = 0.505$. However, the group of four orang-utans monitored at a significantly lower rate than the groups of three individuals: $t(13) = -2.375$, $p = 0.034$ and the paired orang-utans: $t(13) = -2.987$, $p = 0.010$. It is likely that the social relationships within the groups influenced the propensity to monitor conspecifics as the next section examines.

Comparing within species

Within-group social relationships

The species also exhibited marked differences in social relationships. Within dyads, agonism occurred once every three hours in chimpanzees and orang-utans, whereas siamang agonism occurred roughly once per hour. However, siamangs and chimpanzees were characterised by frequent affiliative interactions, and all these dyads engaged in more friendly than agonistic interactions. Orang-utan social relationships varied within dyads, with some dyads characterised by the absence of friendly and presence of agonistic interactions or vice versa.

The association index scores identified strong social relationships based on proximity in certain dyads. Dyads that scored above the 95% confidence interval mean for the species were classed as possessing an affiliative relationship (Table 5.2).

All chimpanzees and siamangs, bar one, possessed at least one strongly affiliative relationship with a conspecific. The orang-utans' affiliative relationships varied according to group. In JT's and female group 2, the only strong relationships were between a juvenile and his mother. In the pair-housed orang-utans (unrelated heterosexual dyads), two of the three pairs possessed an affiliative relationship.

Table 5.2 Results of the association index score on dyadic relationships in chimpanzees, siamangs and orang-utans.

Species	# individuals	# individuals with affiliates	# dyads	# friend dyads
Chimpanzees	6	5	15	4
Siamangs	4	3	6	2
Orang-utans:				
JT group	4	2	6	1
Female group 1	3	0	3	0
Female group 2	3	2	3	1
Allen-Biji	2	0	1	0
Allen-Hati	2	2	1	1
Sulango-Miri	2	2	1	1

Relationship influences on social monitoring

Affiliation. Social monitoring within dyads was positively correlated with the strength of the affiliative relationship (measured by the association index) in chimpanzees: ($n = 15$), $r = 0.77$, $p = <0.001$ and siamangs: ($n = 6$), $r = 0.75$, $p = 0.040$. However, there was a non-significant correlation for the orang-utans: ($n = 15$), $r = 0.29$, $p = 0.301$ (Figure 5.2).

Agonism. The rate of agonism within dyads did not correlate with social monitoring in chimpanzees: ($n = 15$), $r = 0.36$, $p = 0.100$ and siamangs: ($n = 6$), $r = 0.19$, $p = 0.360$. However, a positive correlation was found for the orang-utans: ($n = 15$), $r = 0.47$, $p = 0.040$. This indicated that orang-utan dyads possessing an agonistic relationship (considering the contribution of both dyad partners in agonistic behaviour) engaged in greater rates of social monitoring.

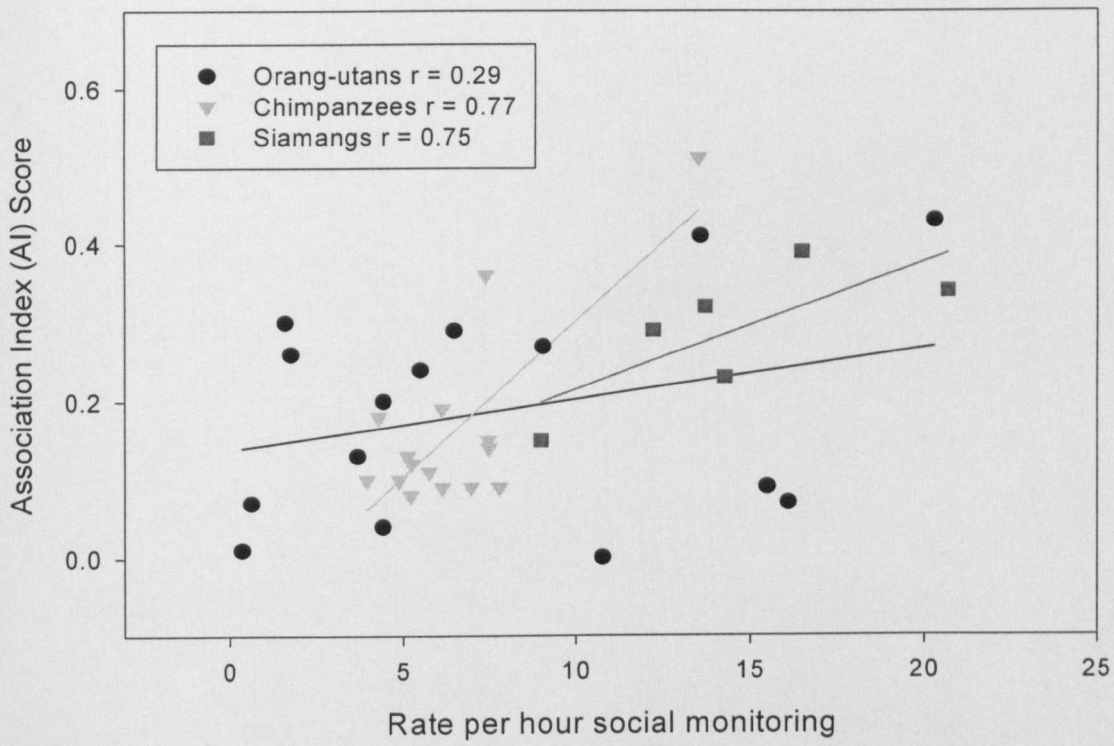

Figure 5.2 The relation between association index score and social monitoring in chimpanzee, siamang and orang-utan dyads.

Monitoring aggressors. Because of the previous non-significant correlations for the siamangs and chimpanzees, an asymmetric matrix was created to identify the relation between each dyad partner's rate of receiving aggression and their rate of initiating social monitoring with each conspecific in the group. Receiving aggression from a conspecific was positively correlated with the rate of monitoring in siamangs (Mantel Z: 131.49, $r = 0.51$, $p < 0.001$) but not for chimpanzees (Mantel Z: 52.29, $r = 0.27$, $p = 0.890$).

To aid comparison with previous studies, each individual's summed rate of social monitoring (regardless of target) was correlated with their individual rate of receiving aggression from all conspecifics. Chimpanzees:

(n = 6), r = 0.23, p = 0.328, and orang-utans: (n = 16), r = 0.34, p = 0.102, that received higher rates of aggression did not engage in higher rates of social monitoring. Siamangs that received high levels of aggression monitored more frequently: (n = 4), r = 0.97, p = 0.015.

Rank. Only chimpanzees possessed a linear rank hierarchy and for this species, rank position was not related to the overall rate of social monitoring initiated: (n = 6), r = -0.17, p = 0.375, or received: (n = 6), r = -0.53, p = 0.278. Within dyads, there was no relation between rank difference and social monitoring (Mantel Z: 412.74, r = -0.03, p = 0.573).

Discussion

The data indicate that social organisation, and specifically the social relationships within species are likely to account for different behavioural correlates of social monitoring in three species of captive apes. Chimpanzee social monitoring was influenced by the strength of affiliative relationships and not by agonism; orang-utan social monitoring was influenced by agonism; and siamang social monitoring was related both to affiliation and aggression received.

Was the attention structure theory supported?

None of the predictions generated by the attention structure theory were strongly supported. Chimpanzees did monitor significantly more than the orang-utans, but this was also true for the siamangs because chimpanzees and siamangs monitored at similar rates. There was also no indication that

the species without rank i.e. acentric groups, engaged in higher rates of non-social monitoring than the chimpanzees i.e. a centripetal group. Although the average rate of monitoring within a dyad of a given species showed variability (especially in the orang-utans), these rates were not significantly different between species. Within chimpanzees, there was no influence of rank position on the frequency of social monitoring.

The similarity in rates of monitoring in chimpanzees and siamangs is contrary to Caine and Marra's (1988) study that reported cooperative and co-dominant relationships in tamarins reduced rates of social monitoring compared to hierarchically organised squirrel monkeys. Additionally, Treves and Baguma's (2002) research with female red colobus and redtailed monkeys suggested that within-group competition and despotic relationships accounted for higher rates of social attention in red colobus females compared to egalitarian female redtailed monkeys during feeding context. In the current study, strong affiliative bonds in both chimpanzees and siamangs may have accounted for comparably high rates of social monitoring and a positive correlation between the association index score and social monitoring.

Why species differences exist in social monitoring

More support for the alternative predictions were found, which considered species differences as a function of the within-group social relationships. Chimpanzees and siamangs monitored at similar rates, and significantly more than the orang-utans. Both chimpanzees and siamangs monitored those they possessed an affiliative rather than an agonistic relationship with,

while orang-utan monitoring was influenced by agonism. These behavioural correlates of monitoring reflected the within-group social relationships i.e. primarily affiliative interactions (chimpanzees and siamangs) or primarily agonistic interactions (orang-utans). The only finding contrary to predictions was the influence of aggression received on social monitoring in siamangs.

Group size

Treves (1999) suggested that as group size increases, social monitoring increases because within-group competition may be higher. It may also be the case that increasing group size simply results in more conspecifics in the group to visually attend to. However, in orang-utans, the rate of social monitoring was actually higher in the smaller groups compared to the larger group (four orang-utans). The data on the siamangs also indicated that more frequent social monitoring (compared to orang-utans) occurred in comparably small groups. Hence, it is unlikely that small group size (maximum of four individuals) solely accounted for low rates of social monitoring in the orang-utans.

Within-group social relationships as a function of species

The results strongly suggest that the quality of the relationships influenced both rates of monitoring when comparing between species, and the behavioural correlates of monitoring within the species.

Chimpanzees. Chimpanzees engaged in relatively high levels of social monitoring, and the strength of affiliation (as measured by the association

index) indicated that social monitoring was related to this affiliative score between dyads. Chimpanzees are characterised by relatively tolerant, egalitarian relations (de Waal, 1982), and possess a flexible social structure (Nishida, 1979). It may be important for chimpanzees with a good relationship to monitor one another. Chimpanzees, especially male affiliates, often form alliances and coalitions against other males (Mitani, Watts, Pepper & Merriwether, 2002b; Watts, 2002). Thus, keeping track of potential alliance partners may have benefits in terms of achieving and maintaining status.

In this study, all correlations between social monitoring and agonism were non-significant. Additionally, contrary to Chance and Jolly's study (1970), rank was not influential on patterns of social monitoring in chimpanzees. Kutsukake (2006) suggested that high behavioural tolerance in chimpanzees may weaken the effect of rank relationships on vigilance. Monitoring conspecifics may be as equally important for high-ranking individuals in order to monitor developing social relationships between other individuals in the group. However, fission-fusion sociality of wild chimpanzees may make this type of monitoring difficult (Mitani et al., 2002a). However, in the current study, it is likely that high levels of cohesiveness and rarity of agonism in this captive environment, meant chimpanzee social monitoring was used to keep track of friends in the group (Dunbar, 1988).

Siamangs. Siamangs possess cohesive and affiliative social relationships with particularly strong bonding between the heterosexual adult pair (Palombit, 1996). In the current study, out of the three species observed, the

siamangs engaged in high rates of monitoring similar to the chimpanzees. Within siamang dyads, partners watched one another at a high rate although not significantly more frequently than the other species. These data are consistent with reports of siamangs synchronising their behaviour, via constant monitoring of each another (Chivers, 1972). Additionally, a high rate of inter-individual proximity (Chivers, 1974) contributes to strong social relationships within a family group of siamangs.

Siamangs that received aggression engaged in increased social monitoring. However, this may be explained by knowledge of social behaviour in Hylobatidae. For instance, most grooming (Chivers, 1972; Gittins & Raemakers, 1980) and agonism (Bartlett, 2003; Chivers, 1972; Gittins & Raemakers, 1980; Lappan, 2007) occurs in the adult-subadult dyad. In siamangs, grooming and aggression are positively correlated (Chivers, 1974; Fischer & Geissmann, 1990). This could explain both affiliative and agonistic behavioural correlates of social monitoring in the current study. The study group of captive siamangs featured two subadult males, which (in wild siamang groups) are usually peripheralised by the adult pair and emigrate from the group (Chivers, 1972; Gittins & Raemakers, 1980). Indeed, the highest rates of social monitoring were initiated by the two subadult males, who also received the most aggression, mainly from the adults. The small number of siamangs in this study made comparisons between the adults and the subadults difficult, but different attention structures may exist between the heterosexual pair compared to the offspring and this merits further investigation. In this group of siamangs,

affiliation and agonism were not necessarily mutually exclusive, thus social monitoring reflected both these behaviours.

Orang-utans. The orang-utans represent a marked contrast from the social organisations of chimpanzees and siamangs. These semi-solitary apes are characterised by an individual fission-fusion social organisation (van Schaik, 1999), and sociality is a result of aggregation at common resources e.g. food or mates (Mitani, Grether, Rodman & Priatna, 1991). However, social relationships between adult orang-utans are generally weak to hostile (e.g. Galdikas, 1984; Maple, 1980; van Schaik & van Hooff, 1996). Orang-utans monitored at significantly lower rates than the chimpanzees and siamangs, but when they did monitor the average rate of monitoring in an orang-utan dyad was similar to the other species. Wild orang-utans are not highly vigilant (Setiawan et al., 1996) and in the current study the frequency of social monitoring in orang-utans was roughly half that observed in the other apes.

Social monitoring in orang-utans was influenced by agonistic relationship quality. Orang-utans monitored those with whom they engaged in more frequent agonistic interactions, either as initiator or as recipient. This may be because avoidance of conspecifics is an important social behaviour for orang-utans (van Schaik, 2004). Unlike the chimpanzees and siamangs that may use social monitoring to keep track of affiliates, the orang-utans may use monitoring to avoid other orang-utans, particularly those with whom an individual possesses an agonistic relationship. The non-significant result of aggression received on social monitoring suggests that overall agonistic

interactions within a dyad, rather than aggression received, influences monitoring in orang-utans.

The difficulties in interpreting orang-utan social monitoring pertain to the small group sizes and group composition. Two out of the three heterosexual pairs were classed as having an affiliative relationship, yet social monitoring varied markedly in these friendly heterosexual pairs. Weak social relationships in orang-utans do not negate the need to monitor conspecifics (Kaplan & Rogers, 2002); however, low frequencies of social interactions in orang-utans may have contributed to reduced monitoring in comparison to the other apes.

Methodological issues

Social monitoring is often studied in captive populations with groups of less than eight individuals (Caine & Marra, 1988; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998; Pannozzo et al., 2007; Strayer & Gariepy, 1986; Torres de Assumpção & Deag, 1979). In the current study, group sizes ranged from two to six individuals, but overall the group sizes were considered representative of the species in question. Siamangs live in family units of up to six individuals in the wild (Chivers, 1972; 1974; Gittins & Raemakers, 1980; Lappan, 2007) and in captivity (Fischer & Geissman, 1990; Orgeldinger, 1991). Captive orang-utans are usually housed in uni-male small groups, or heterosexual pairs because of their semi-solitary nature and hostile male-male relationships (Maple, 1980; Perkins, 1992). Chimpanzees live in large communities (Nishida & Hiraiwa-Hasegawa, 1987; Stumpf, 2007), consisting of up to 150 individuals (Watts, 2002).

Communities fission into smaller temporary parties, usually less than six individuals (Nishida & Hiraiwa-Hasegawa, 1987). In the current study, the captive chimpanzee group was thought to be comparable to a party; however, there were no changes in party composition in the captive setting that would be observed in a free-ranging population. The small captive group also meant that dyads of varying sex composition could not be compared.

Because only one group of siamangs and chimpanzees were studied, the results may not generalise to other groups of these species. The orang-utan data with multiple groups indicate that frequencies of social monitoring vary with group composition. It is also possible that monitoring within the siamang adult pair will be different to that observed in other dyads.

Few data exist on social monitoring in apes. While orang-utan (Kaplan & Rogers, 2000; 2002) and gorilla (Watts, 1998) social monitoring has been examined, comparative perspectives in apes are lacking. Approaches such as Caine and Marra's (1988) study would help identify firstly, the frequencies of social monitoring in different species, and secondly, whether social monitoring reflects social organisation and the social relationships of the species.

Overall conclusions

The results suggest variability in the basis of social monitoring in three captive ape species. Generally, the results reflect the social relationships evident in the species. When social relationships were primarily affiliative, social monitoring occurred at a greater rate, and affiliation was correlated with social monitoring (chimpanzees and siamangs). When social

relationships were weak, monitoring occurred at a lesser frequency, and was related to agonism (orang-utans). In siamangs, the influence of aggression received (in addition to affiliation) on social monitoring may have been related to increased aggression in grooming dyads (Chivers, 1972; Fischer & Geissmann, 1990). There was little support for the attention structure theory (Chance, 1967; Chance & Jolly, 1970), particularly the predictions relating to centric vs. acentric species.

Social monitoring reflects the social dynamics and organisation of the group and species. The role of affiliation on social monitoring has been largely neglected, even though affiliation may account for patterns of social monitoring to a greater extent than agonistic or competitive influences (Strayer & Gariepy, 1986). Further research needs to evaluate the influence of multiple social variables on social attention to capture the dynamic qualities of social behaviour and identify the underlying basis of monitoring in a variety of species.

CHAPTER 6

USING VISUAL ATTENTION TO REFERENCE CONSPECIFICS IN CAPTIVE ORANG-UTANS

Overview

In this chapter, I evaluate the role that visual attention to conspecifics may play in learning to react and respond appropriately to ambiguous events. This phenomenon known as social referencing has been experimentally studied in young primates, but information on whether social referencing occurs in response to naturally occurring events, in a captive environment, in older individuals, or in orang-utans is unknown.

Some outstanding issues pertaining to social referencing behaviours were assessed by considering social referencing observationally in the context of naturally occurring events (study 1) and by measurement of visual responses based on the familiarity and biological relevance of playback vocalisations (study 2). This chapter provides information on events that elicit social referencing behaviours and addresses whether the salience and ambiguity of events influence the propensity to reference conspecifics in both adult and immature orang-utans.

Dissemination of research from this chapter

Lane, Bard & Reddy (2005). Naturalistic social referencing in captive orang-utans International animal social learning conference, June 15-18, St Andrews, UK.

Introduction

Social referencing is a well studied visual behaviour in human infants (reviewed in Boccia & Campos, 1987; Feinman, Roberts, Hsieh, Sawyer & Swanson, 1992). Classically, visual referencing of individuals serves to reduce uncertainty, thus information gained from visually attending to another individual can be used in order to react or appraise a situation appropriately. Social referencing comprises two components: a) information seeking using referential looks alternating between another individual and an object/event; and b) behavioural regulation, evidenced by subsequent behaviour matching the information received from the referent (Hornik & Gunnar, 1988).

Most knowledge on this phenomenon comes from laboratory studies involving ambiguous events, such as the visual cliff paradigm (Sorce, Emde, Campos & Klinnert, 1985), presentation of novel objects (Hornik, Risenhoover & Gunnar, 1987; Walden & Ogan, 1988; Walden & Baxter, 1989) or the presence of a stranger (Feinman & Lewis, 1983). If a more experienced individual provides positive affective information, a human infant is more likely to cross a visual cliff or smile at a stranger (Feinman & Lewis, 1983; Sorce et al., 1985) or interact with a novel toy (Hornik et al., 1987; Walden & Baxter, 1989) than if negative or fearful information is provided.

Social referencing is implicated as a social information gathering process yet differentiation is made between simpler explanations of stimulus exploration seen in some mammalian species from the 'capacity to exploit social channels of information about the world' (Baldwin & Moses, 1996, p. 1917). In considering the cognitive basis of referencing, Feinman et al.

(1992) postulate that social referencing is more than merely reacting to stimuli; the referrer must be capable of appraising the situation. The ability to seek information from those more experienced may therefore be adaptive.

The evidence for social referencing in non-human primates

Non-human primates show evidence of the ability to exploit social sources of information, as seen in tactical deception (Whiten & Byrne, 1988), formation of coalitions and alliances (Cords, 1997), conflict resolution (Cords, 1997; de Waal, 1989), and cooperation (Silk, 2005). Therefore, given primate social complexity, social referencing may be an important component of learning about the environment, which has clear adaptive benefits.

Social referencing differs from social monitoring. Although social monitoring and social referencing both involve visual attention towards a conspecific, in social referencing, attention is alternated between an individual and an object/event. Boesch & Boesch-Achermann's (2000) observations of wild chimpanzees suggest that some form of referencing may be used when an unhabituated animal joins a habituated group and accepts human presence rapidly. Young snake-naïve rhesus monkeys rapidly acquire a fear of snakes after observing their parents (Mineka, Davidson, Cook & Keir, 1984) and unrelated conspecifics (Cook, Mineka, Wolkenstein & Laitsch, 1985) responding fearfully. Infant chimpanzees' behaviour matches their mother's behaviour after the presentation of novel objects (Itakura, 1995). Although these studies indicate some form of behavioural regulation, they inform little about the visual component of social

referencing i.e. how visual attention is modulated between an object and an individual in this appraisal process.

The most detailed study on social referencing in primates (Russell et al., 1997) investigated both behaviour regulation and alternation of visual attention in infant chimpanzees in response to a novel object. All chimpanzee infants used both referential visual attention between the object and caregiver, and regulated their behaviour in response to the emotional information received from a human caregiver. Chimpanzees withdrew from the object more frequently when a fearful message was given by the caregiver and looked for longer when a positive message was given.

A recent study on social referencing in free-ranging macaques using a toy snake, found referential looking did not occur in the majority of infants (Roberts, McComb & Ruffman, 2008). This suggests that the majority of infants may have appraised the snake themselves without reference towards their mother. However, non-referential looks i.e. social monitoring occurred more frequently in the presence of the snake compared to a control period. In this case, some information may have been gained from monitoring the mother; however, the absence of gaze alternation and behavioural regulation suggests the infant was not actively seeking information on how to respond.

The salience of events/stimuli in eliciting referential attention

Primate studies such as Mineka et al. (1984) and Cook et al. (1985) suggest that biological relevance rather than perceived ambiguity may be important when learning to react appropriately. Indeed, in bonnet macaques, an ambiguous and biologically relevant object such as an upside-down-leopard

facilitates increased looking at conspecifics compared to an unambiguous upright leopard (Coss & Ramakrishnan, 2000).

In human infants, social referencing occurs in response to the presence of both social influences e.g. a stranger (Feinman & Lewis, 1983) and non-social stimuli e.g. visual cliff (Sorce et al., 1985) or presentation of a novel toy (e.g. Hornik & Gunnar, 1988). Similarly, in non-human primates, although social referencing is often tested in laboratory studies with inanimate objects (Itakura, 1995; Russell et al., 1997), social referencing may also contribute to the evaluation of social relationships. Juvenile chimpanzees discern their mother's social relationships through some unspecified process, and adjust their social behaviour accordingly (Evans & Tomasello, 1986).

Some important issues in social referencing research

The stimuli used to elicit social referencing may be particularly important. As Feinman et al. (1992) argue, interactions with strangers and with novel objects are ecologically relevant and frequent occurrences in a child's daily life. However, most primate cognitive adaptations and problem solving are specific to the social domain and to a lesser extent within the physical domain (Cheney & Seyfarth, 1990). Therefore comparison of both environmental and social referents would clearly further knowledge of social referencing.

Infant social referencing research is generally restricted to laboratory settings; therefore it is unclear how referencing functions in everyday life

(Feinman et al., 1992). It is possible that other individuals apart from the mother could serve as referents (Hirschberg & Svejda, 1990).

Primates have not been rigorously tested for social referencing naturalistically, that is, in a familiar and socially orientated environment. Evidence from Evans and Tomasello (1986) and Boesch and Boesch-Achermann (2000) would suggest that naturalistic social referencing occurs. However, social referencing is a relatively infrequent event (Feinman et al., 1992). In a natural setting, given the dynamic nature of primate social groups, both naturally occurring environmental and social events may provoke referencing behaviours. In this case, the novelty/frequency of naturally occurring events may be important to consider. If social referencing is linked to ambiguity, then rare/novel events that are not often encountered would be expected to facilitate social referencing. Proof of this may be established by the documentation of baseline levels of referencing behaviours (Baldwin & Moses, 1996) to permit the comparison of looking at a novel event to a familiar one or no event at all.

A final issue concerns the influence of age on the seeking of information. Social referencing is usually associated with uncertainty and inexperience; therefore, only young individuals may require information from more knowledgeable individuals on how to appraise a situation. There are few data examining social referencing in human adults, although Feinman et al. (1992) assert that referencing processes encompass a broader knowledge acquisition process throughout the lifespan.

Why study social referencing in orang-utans?

The evidence so far suggests that social referencing processes occur in both hominoids and anthropoids so it is also expected in orang-utans. Although adult orang-utans are semi-solitary in the wild (Galdikas, 1984; MacKinnon, 1971; 1974), in most zoos, orang-utans are kept in small groups (Maple, 1980). This means that in a captive group, there may be more than one individual from whom to seek reference. However, the protracted mother-offspring relationship in orang-utans coupled with little contact and interaction with other adults (Galdikas, 1984; van Schaik & van Hooff, 1996) emphasises an infant's reliance on the mother as a vital and, more importantly, the main source of information for a young orang-utan.

Captive populations of orang-utans provide valuable opportunities to assess orang-utans in group situations that may be difficult to observe or rare in the wild. Large naturalistic enclosures at Zoo Atlanta provide: a) ecologically relevant stimuli (the presence of multiple orang-utans, conspecifics within the same exhibit, and visual access to orang-utans in different exhibits) and b) naturally occurring social and non-social events. Observing orang-utans' visual responses to naturally occurring events in their environment provides an important baseline indication of naturalistic social referencing.

Study 1 was carried out to take a first look at whether social referencing occurs in response to naturally occurring events. Social referencing can only take place if a stimulus or event is firstly attended to. Therefore, it was considered important to determine if: a) orang-utans visually attend to naturally occurring events and b) whether a conspecific is

immediately looked at after visually attending towards an event (referential looking). Visual attention towards events and subsequently to conspecifics was predicted to vary according to the ambiguity and the biological relevance of the event. Rarely occurring events were predicted to be more ambiguous based on their novelty and therefore would be visually monitored more frequently than banal events. Additionally younger orang-utans were expected to visually attend to rare events more frequently than older orang-utans, and to engage in social referencing.

STUDY 1: NATURALISTIC SOCIAL REFERENCING

Methods

Study species

Subjects were 10 captive orang-utans at Zoo Atlanta (see chapter 5). In this chapter, the young dependant infant in Sulango's group (Satu) was included.

Data collection

The orang-utans were observed throughout the day during March 2005. Two digital video cameras (Canon MVX 750i and Panasonic NVGS35) were used to record the orang-utans' behaviour. One video camera was handheld and zoom focused the face of the focal animal. The second video camera (Canon) equipped with a wide-angle lens, was stationary upon a tripod and captured the social and environmental context. Enhanced audio abilities of the video cameras allowed even low sounds to be captured. Additional narration during the video recording by the experimenter supported the video evidence and clarified distant or rare events.

Data Coding

Classification of events

Naturally occurring events were coded as rare, unusual or banal based on previous experience of studying the orang-utans at Zoo Atlanta from 2003-2004, and from the observational period of this study. These events were also considered based on being a social event or an environmental event.

Event novelty. Rare events were coded based on rarity either in this study or at previous observations at Zoo Atlanta. Unusual events occurred infrequently while banal or regularly occurring events occurred more than once a day.

Event type. Environmental events were human related (e.g. presence of keeper), auditory (e.g. building maintenance, training clickers, jangling of keys, sound of radios) or visual (e.g. airplanes, birds, dynamic structures in exhibit). All events pertaining to orang-utans were classified as social. These social events originated from outside the social group, such as long-call displays (extra-group), and from within the social group, such as aggression, approaches and orang-utan movement that occurred within 10m of the focal animal (intra-group).

Response to naturally occurring events

Once an event occurred, orang-utans were assessed as responding to the event by head and/or eye re-orientation to the event location during the event or within two seconds of the event ceasing.

Social referencing

Social referencing was defined as attention alternated between the event location and a conspecific. As defined by Russell et al. (1997) social referencing was scored when attention to a conspecific was: a) preceded by (in the previous two seconds) a look to the event location and/or b) followed by (within two seconds) a look to the event location.

Results

The frequency of events occurring within an orang-utan's focal period varied according to individual, thus results are summarised as percentages of events and analysed using t-tests.

Event novelty and monitoring

Rare events

These types of events were uncommon but always involved subsequent visual monitoring of the event. Rare events occurred approximately once every 10 hours.

Unusual events

Responses to unusual events varied as a function of the event characteristics (see the next section for event type) and individual differences existed (Figure 6.1). Averaged across orang-utans, roughly 70% of unusual events were visually attended.

Banal events

Banal events were highly frequent (often irrelevant) environmental stimuli that appeared to be tuned out by the orang-utans, as only approximately 39% of banal events were visually attended. This was a significantly lower visual response compared to unusual events: $t(9) = -4.395$ $p = 0.020$.

Nine out of the 10 orang-utans showed the same pattern of response, with more frequent visual responses to unusual events compared to banal ones. The youngest orang-utans did not appear to visually respond to naturally occurring events differently to the other orang-utans.

Event type and monitoring

Environment events

Several comparisons were conducted to determine the relevance of social compared to environmental events. Unusual environmental events were attended to significantly more frequently than banal environmental events: $t(9) = 4.131$, $p = 0.003$, see Figure 6.2.

Social events

Intra-group social events occurred more frequently than extra-group social events and extra-group social events were monitored significantly more frequently: $t(5) = 3.626$, $p = 0.015$. These findings suggest that event novelty and event type influences visual response.

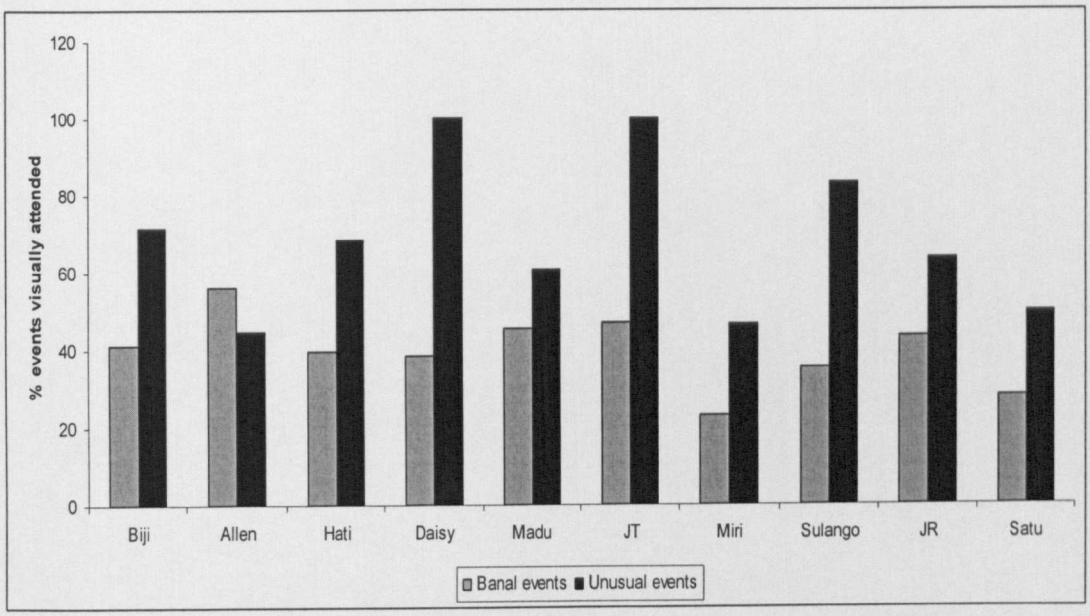

Figure 6.1 Percent of banal and unusual events attended to by the orang-utans (in descending order of age from left to right).

Comparison of environment and social events

Banal environmental events were monitored significantly less than both intra-group: $t(9) = -2.534$, $p = 0.032$ and extra-group social events: $t(5) = -9.354$, $p = <0.001$. There were no differences in responses to unusual environmental events compared to intra-group social events: $t(9) = 1.113$, $p = 0.295$. However, unusual environmental events were monitored significantly less than extra-group social events: $t(5)= -3.163$, $p = 0.025$.

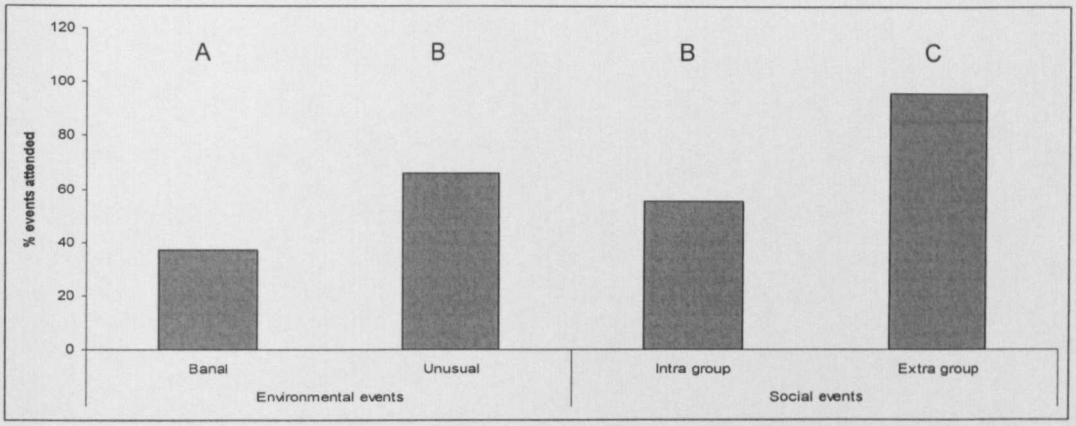

Figure 6.2 Percent of environmental and social events attended to by the orang-utans (different letters denote significant differences between events).

Social referencing

In total, four instances of social referencing occurred (Table 6.1). These instances of social referencing occurred in the youngest orang-utans. After visually attending to the event, attention was immediately directed towards a conspecific whose affect or behaviour was typically neutral. The orang-utans could have received information from the referee that there was little to worry about, however, in the two instances where the mother was referenced, proximity to the mother was also sought.

Table 6.1 Social referencing in orang-utans in response to naturally occurring events.

Subject	Class	Age	Event	Event novelty	Referee
Satu	Infant	1	Building work	Unusual	Mother
JR	Juvenile	2.5	Long call	Unusual	Mother
JR	Juvenile	2.5	Loud machine	Unusual	Adult female
Sulango	Unflanged male	13	Unfamiliar bird in exhibit	Rare	Adult female

Discussion

Social referencing occurred rarely in the naturalistic zoo setting. Rare or unusual environmental and social events were visually attended by the 10 orang-utans. Actual response or attention directed towards an event varied according to individual proclivities, but the more novel an event, the more likely it was to be visually attended.

In laboratory experiments with human infants, social referencing is associated with an ambiguous event. It is thought that uncertainty prompts an individual to refer to another to assist with appraising the situation. The evidence presented in this study supports the idea that novel and potentially ambiguous events are important. Unusual events received greater attention compared to banal events; additionally, no instances of social referencing were observed for banal events.

Primate studies also emphasise the importance of biologically relevant stimuli coupled with ambiguity in information seeking, e.g. Roberts et al. (2008). The orang-utans' frequency of attending to events pertaining to conspecifics outside the group, especially long calls, supports the suggestion that biological relevance is important to consider. The fact that social referencing occurred infrequently also suggests that orang-utans may have appraised the event themselves without referencing others. It is not known whether this is what orang-utans do, or whether the event was perceived as unambiguous or biologically irrelevant. Events pertaining to orang-utans outside the social group generally received the most attention: all orang-utans that heard a long call oriented in the direction of the vocalisation and the juvenile engaged in referential looking upon hearing this event.

The influence of novelty and salience on information seeking was considered further in study 2. Playback vocalisations of long calls and kiss squeaks were explored further because they constitute biologically relevant stimuli; occur naturally in the Zoo Atlanta orang-utans; and were salient for the orang-utans given that all individuals that heard a long call in study 1 orientated to the call. Playback experiments of vocalisations also provide a means of manipulating the ambiguity of an event whilst maintaining a naturalistic context.

STUDY 2: EXAMINING THE INFLUENCE OF FAMILIARITY AND BIOLOGICAL RELEVANCE ON INFORMATION SEEKING

Study 1 demonstrated that orang-utans responded visually and reliably to long calls. The goal of study 2 was to examine if playback vocalisations could elicit social referencing in orang-utans. Specifically, if there is a greater frequency of looks directed to conspecifics post-playback and whether these post-playback social looks are referential. Looks directed towards the location of the speaker and to conspecifics in the pre-playback period will be used as a control to determine whether the playback elicits significantly more visual orientating to the location of the speaker and attention to conspecifics.

Vocalisation type was predicted to influence information seeking behaviours. Kiss squeaks are used to signal mild worry or annoyance (MacKinnon, 1971; 1974); while long calls serve a spacing function between adult males (Mitani, 1985), are used in response to disturbance (MacKinnon, 1974) and to attract females (Mitra Setia & van Schaik, 2007). Responses of wild orang-utans are much stronger towards long calls than to kiss squeaks

(MacKinnon, 1971; 1974; Mitra Setia & van Schaik, 2007; Delgado, personal communication). Additionally, responses of females and infant orang-utans to long call vocalisations are greater if the male is unfamiliar rather than familiar (Mitra Setia & van Schaik, 2007; van Schaik, 2004; Delgado, personal communication).

Accordingly, long calls were predicted to evoke the greatest visual response in terms of looks directed to the location of the vocalisation, and to conspecifics. If novelty/ambiguity is important as demonstrated in study 1, vocalisations from unfamiliar individuals should provoke more uncertainty, and social referencing may occur more frequently. Finally, if social referencing is associated with uncertainty, the greatest propensity to seek reference should be observed in younger orang-utans.

Methods

Study species

Eight out the 10 captive orang-utans from study 1 were observed in study 2. Due to medical procedures, an adult female (Hati) and adult male (JT) were not part of this study.

Playback vocalisations

Playback stimuli consisted of two types of orang-utan vocalisations: long calls and kiss squeaks. To examine the effect of novelty and ambiguity, three long calls (one from a wild orang-utan and two from Zoo Atlanta orang-utans Allen and Chantek) were used as stimuli. In study 1, Allen long called approximately once a day while Chantek long called infrequently (and did not

in study 1). Therefore, in terms of novelty, the wild orang-utan's call was considered the most novel and unfamiliar, Chantek's call less novel but familiar, and Allen's call the least novel and most familiar. Two kiss squeaks were also used as comparison stimuli to examine the influence of salience on orang-utan information seeking (one from a wild orang-utan and one from Sulango, a young male at Zoo Atlanta).

Vocalisations from wild orang-utans were obtained from the British sound library and vocalisations from the Zoo Atlanta orang-utans were recorded opportunistically during August 2006 using a Sennheiser ME67 directional microphone and cassette recorder. For each vocalisation type, playback sequences were similar in vocalisation length and decibels. Vocalisations were broadcast from a Sony CDF-ZW755 portable stereo, placed on the edge of the exhibit walls (in an area only accessible by staff) approximately 10m away from the orang-utans.

Experimental protocol

A within subjects design was used, with each orang-utan receiving five playback vocalisations on five separate occasions (three long calls and two kiss squeaks). The orang-utans received the playback vocalisations either early in the morning or late in the afternoon. This strict schedule was necessary to ensure that the first group out in the morning participated in the experiment, and there were no other orang-utan groups in adjacent out-door exhibits that could hear and become habituated to the playbacks. Similarly, when all the other orang-utan groups were brought into the indoor holding for the night, the last group remaining outside would receive the playback. The

schedule for letting out groups in the morning and leaving them in the outdoor exhibit in the late afternoon was alternated according to the experimental schedule.

Five minutes of silence preceded all the playback vocalizations; this gave the observers opportunity to play the vocalisation recording (including the 5 minutes of silence) and then take position with the video cameras. For each vocalisation presentation, there were as many video cameras as orang-utans. One observer maintained a focal video camera in the staff only area, and a second observer in the public area of the exhibit operated another focal video camera. A third wide angle camera was also stationed in the public area to capture the overall context. To prevent habituation to the playback procedure, no more than one vocalisation was broadcast to a group per day.

Data analysis

Responses occurring in the one-minute period post-playback (including the time whilst the playback stimulus was still being broadcast) were examined for social referencing. The one-minute period prior to playback was used as a control period.

For both the pre- and post-playback periods, three different responses were coded: the number of looks toward the speaker/vocalisation, the number of looks towards a conspecific and social referencing involving alternating attention between a conspecific and the vocalisation. As was the case in study 1, social referencing was scored if a look to the speaker was followed by a look towards a conspecific within two seconds and/or a look

towards a conspecific was followed within two seconds with a look to the speaker.

The data were analysed using repeated measures ANOVA's and t-tests. Pearson's correlations were used to examine the relation between age and social referencing behaviours.

Results

Orienting to the vocalisation

The orang-utans response towards the speaker playing the vocalisations were analysed for each vocalisation separately compared to the control period. For all conditions, the frequency of orienting to the speaker was greater in the experimental period than the control period.

Long calls

The highest frequency of orientating was evident for the long calls, particularly the recording of Allen's and the unfamiliar long call, with a mean of five looks towards the speaker. In contrast, orang-utans rarely looked towards the general location of the speaker during the control period, resulting in a significant increase in looking towards the speaker during the experimental period: Allen's long call: $t(7) = 5.401$, $p = <0.001$; Chantek's long call: $t(7) = 6.545$, $p = <0.001$; unfamiliar long call: $t(7) = 8.367$, $p = <0.001$. There was no difference in frequency of orienting between the three long calls: $F(2,14) = 0.212$, $p = 0.811$.

Kiss squeaks

Less frequent visual orientating was evident when kiss squeaks were broadcast, with a mean of three looks directed towards the speaker. However, there were significant differences in orienting towards the speaker during the playback vocalisations compared to the control period: unfamiliar kiss squeak: $t(7) = 3.347$, $p = 0.006$; Sulango's kiss squeak: $t(7) = 7.561$, $p < 0.001$. There was no difference in visual response between the two kiss squeak vocalisations: $t(7) = -1.377$, $p = 0.105$.

Looks towards conspecifics

Looks directed towards conspecifics were coded in order to determine if conspecifics were used as a point of reference during vocalisation playbacks compared to the control period.

Long calls

The long calls from the two familiar orang-utans elicited the most looking at conspecifics. Approximately three looks towards conspecifics (range 1-8 looks) were observed post-playback for Allen's long call, and two looks (range 0-5 looks) for Chantek's long call. These looks to conspecifics occurred significantly more frequently in the experimental period compared to the control period for all long calls: Allen's long call: $t(7)=2.393$, $p = 0.024$; Chantek's long call: $t(7) = 1.925$, $p = 0.004$; unfamiliar long call: $t(7) = 2.646$, $p = 0.016$ (Figure 6.3).

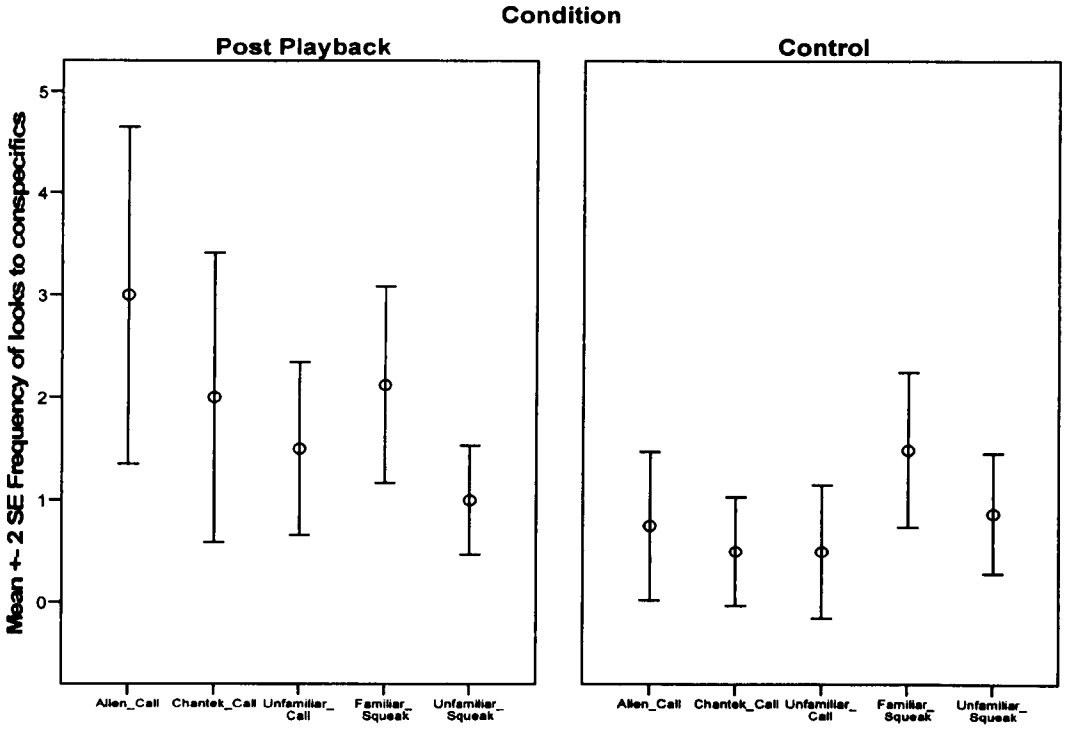

Figure 6.3 Orang-utans' frequency of looks to conspecifics during the playback conditions.

There were no significant differences in the frequency of looking at conspecifics between the three long call vocalisations: $F(2,14) = 1.885$, $p = 0.094$. However, younger orang-utans looked more at conspecifics following the unfamiliar long call: ($n = 8$), $r = -0.67$, $p = 0.034$, while there was no relation between age and looking at conspecifics for Allen's long call: ($n = 8$), $r = -0.34$, $p = 0.202$ or Chantek's long call: ($n = 8$), $r = 0.40$, $p = 0.162$.

Kiss squeaks

A higher frequency of looks towards conspecifics occurred during the experimental period than the control period. Kiss squeaks from an unfamiliar orang-utan elicited approximately one look, while kiss squeaks from Sulango resulted in approximately two looks post-playback (Figure 6.3).

Despite there being differences between the control and experimental periods in orientating to the speaker, the increase in looks to conspecifics was not significantly different from that observed in the control period compared to the experimental period: Sulango's kiss squeak: $t(7) = 1.049$, $p = 0.164$; unfamiliar kiss squeak: $t(7) = 0.552$, $p = 0.299$. Therefore, only long calls are analysed further.

Social referencing elicited by long calls

All orang-utans engaged in referential looking in response to the playback at least once, that is attention was alternated between the location of the vocalisation and a conspecific (see Table 6.2 for a summary). Referential looking varied according to the vocalisation. Allen's long call elicited an average of 2.5 referential looks and seven out of the eight orang-utans engaged in referential looking in response to this vocalisation. The unfamiliar long call elicited 1.13 referential looks, in seven out of the eight orang-utans. The lowest frequency of referential looking was observed in response to Chantek's long call (0.88 referential looks) and three out of the eight orang-utans engaged in referential looking during this long call. There was a trend of long call identity on the frequency of referential looks: $F(4,14) = 3.166$, $p = 0.073$.

Age and referential looks

For the unfamiliar long call, the number of referential looks were negatively associated with age: $(n = 8)$, $r = -0.63$, $p = 0.049$, as younger orang-utans showed a greater number of alternating looks between a conspecific and

vocalisation. However, this was not the case for Allen's long call: (n = 8), r = -0.33, p = 0.214; nor for Chantek's long call: (n = 8), r = -0.28, p = 0.255.

Using information received from social referencing

In most cases, the orang-utans showed little behavioural change in their responses to the long calls (although see the next section for strong behavioural reactions in mothers). Consequently, little behavioural regulation based on information received from referencing was observed. During Allen's long call, one adult female moved closer to the vocalisation after referencing another adult female showing neutral affect, and the young male withdrew from the vocalisation area after witnessing a conspecific reacting negatively.

Referencing in the mother-offspring dyad

Social referencing in the two mother-offspring dyads did not occur frequently. Upon hearing Allen's long call, both mothers immediately grabbed their offspring (either an infant or juvenile) before the youngsters could even react. Contact was maintained whilst the vocalisation was being broadcast, thus visual referencing of the mother did not occur in the juvenile or infant. The juvenile, whilst in contact with his biological mother, also referenced another female who was behaving neutrally.

For the unfamiliar long call, both youngsters were out of proximity from their mother. The infant withdrew from the vocalisation area without reference to his mother (reference occurred after withdrawing), while the juvenile remained stationary and looked referentially at his mother from a distance.

Similarly, upon hearing Chantek's vocalisation, the infant reached out to his father, however, as his father immediately moved away to monitor the vocalisation, the infant then contacted his mother and no visual referencing of her occurred. These findings suggest social referencing may also take a tactile form. Specifically, if an individual is in contact with their mother, tactile social referencing from cues such as posture or tenseness may be utilised instead of visually mediated cues (see Bard, 1992, Bard et al., 2005 for reduced gaze alternation when in contact to the mother).

Table 6.2 Percent of orang-utans in each age-sex class that engaged in referential looking.

	Long call vocalisation		
Orang-utan classes	Unfamiliar	Allen	Chantek
Flanged male N=1	100%	100%	0%
Adult females N=3	66%	100%	33%
Unflanged male N=1[a]	100%	100%	100%
Young female N=1	100%	100%	100%
Infant[a]/juvenile[a] N=2	100%	50%*	0%*
% of orang-utans engaging in referential looks	87%	87%	37%

[a] Engaged in naturalistic referencing study 1
*Tactile referencing may have occurred in the absence of referential looking

Referential looks in adults

Adult orang-utans used referential looking, particularly during Allen's and the unfamiliar long call. All adults referenced another adult, despite a large distance between them and generally neutral affective information being received. The strongest responses to the playbacks were observed in a

young unflanged male; he also engaged in the greatest number of referential looks. Upon hearing all vocalisations, he immediately climbed the nearest structure to the vocalisation location, and alternated gaze between the vocalisation and his female partner from an increased height. Roughly, three minutes post-playback of Allen's and the unfamiliar long call, this young male engaged in a threat display: pilo-erection, strutting, rocking, shaking ropes and kiss squeaking which had not been observed previously in this individual during this study or other studies conducted with the Zoo Atlanta orang-utans.

Discussion

All orang-utans engaged in social referencing in response to a long call vocalisation at least once. All long call types were attended to equally: an orang-utan was as likely to orient to a familiar long call as a call from an unfamiliar individual. Importantly, significantly more social looking occurred during the long call playback condition than the control period. In chapter 5, orang-utan social monitoring occurred infrequently; however, upon hearing a long call vocalisation, social monitoring increased three-fold at least. Many of these looks were referential, that is, attention was alternated between the vocalisation location and a conspecific. Although there was no significant difference between the long call vocalisations on the frequency of referential looks, younger orang-utans alternated their gaze more frequently when the vocalisation was an unfamiliar long call compared to long calls from familiar individuals (Allen and Chantek). The results from study 2 highlight several important findings: that adult and young orang-utans reference conspecifics;

that social referencing occurs in response to biologically relevant stimuli; and that social referencing occurs in a zoo setting.

General Discussion

Zoo living orang-utans were visually attentive to unusual naturally occurring social and environmental events. Social referencing however, occurred rarely in response to these naturally occurring events and only in the three youngest orang-utans. Nevertheless, all orang-utans (adults, a juvenile and an infant) engaged in social referencing at least once in response to long call vocalisations. Looks used to localise the vocalisation and looks to conspecifics occurred significantly more often during and after the playback (compared to the control period). The importance of novelty and biological relevance on the propensity to reference a conspecific are highlighted by these studies.

Salience of the event – biological relevance, ambiguity and novelty

Social referencing is typically associated with ambiguity (Feinman et al., 1992) in part because the referring individual may lack the necessary knowledge and/or experience to appraise an uncertain event. The captive environment can be predictable and it is highly likely that all orang-utans had extensive experience of the irrelevance of some naturally occurring events, e.g. visitors, and appraised events without reference to others. Unusual events, however, provoked more visual orientating, and a small number of referencing behaviours in the youngest orang-utans. However, for instance, when there was a loud explosion at the zoo (a one-off alarming event), the

focal adult orang-utan at the time did not seek reference either before or after orientating to the noise.

Some studies (Cook et al., 1985; Mineka et al., 1984; Roberts et al., 2008) suggest the perceived biological relevance of stimuli/events may be more conducive for information seeking. However, some biologically relevant stimuli (especially predator stimuli) are so unambiguous that the flight response is immediate without any reference to conspecifics, while presentation of an inverted leopard may invoke uncertainty and consequently more looks to conspecifics (Coss & Ramakrishnan, 2000).

Long call vocalisations were considered as biologically relevant, as long calls are an important means of communication in free-ranging populations (Delgado & van Schaik, 2000; MacKinnon, 1971; 1974; van Schaik, 2004). In free-ranging orang-utans, responses to long calls vary according to familiarity, the level of threat and the relationship with the caller (Delgado & van Schaik, 2000; Mitra Setia & van Schaik, 2007; van Schaik, 2004). For instance dominant males often approach long calls to chase the caller (van Schaik, 2004), while subordinate males avoid long calls (Mitani, 1985). Females may respond fearfully to long calls of unfamiliar males or unlikely sires (Galdikas, 1984; van Schaik, 2004; Delgado, personal communication).

Naturally occurring long calls at Zoo Atlanta were visually attended by all individuals that heard them, but only a juvenile sought reference (study 1). However, all orang-utans referenced at least once during the long call playbacks (study 2). The playback vocalisations did not provide evidence for a clear effect of familiarity or ambiguity on visual orientation to the call, since

the frequency of social monitoring, and referential looking were similar for the unfamiliar and familiar long calls. There was also little evidence that the long calls were avoided according to familiarity, as most orang-utans remained stationary whilst visually orientating. However, the threat display by Sulango to Allen's and the unfamiliar orang-utan's long call, suggests Sulango was responding aggressively.

It is likely that the familiar long calls were more ambiguous to the orang-utans than anticipated. Typical responses to long calls observed in study 1 involved orientating in the direction of the sound and usually sighting the calling orang-utan, while in study 2, there was no visible orang-utan producing a long call and the sound was coming from an area where neither Chantek nor Allen resided. Thus, in this sense, all long calls may have been considered by the orangutans as equally ambiguous, and the data support this interpretation. Broadcasting the vocalisation from Chantek's or Allen's exhibit would confirm whether the location of the playback is important when considering ambiguity, and whether deviation from normal occurrences, e.g. the location, influences the referencing response.

Age and referencing

Social referencing allows an individual to learn the meaning of objects and social interactions based on information that is beyond their own experience. The rare incidences of naturalistic social referencing occurred in the youngest orang-utans. However, for playback of familiar long calls, there were few differences between younger orang-utans and older orang-utans in referencing conspecifics. For the unfamiliar vocalisation, young orang-utans

tended to show a greater frequency of gaze alterations between the location of the vocalisation and a conspecific. This may have been the first time that the young orang-utans heard a long call from a male other than Allen or Chantek. Although all the older orang-utans were captive born, they may have had more experience with male orang-utans, for example at a different zoo. This age effect in response to the most ambiguous and novel long call suggests that information was being sought (at least for the younger individuals).

The most striking finding was that adult orang-utans looked significantly more at conspecifics and used referential looks during the playback period compared to the control period. Feinman et al. (1992) emphasised the role of social sources of information in interpreting the environment and how the referencing process operates throughout life. It is unclear whether orang-utans used social referencing to gather information from conspecifics on how to react or whether it was a check to confirm if the other orang-utan reacted to the vocalisation. Boesch and Boesch-Achermann's (2000) observations suggest that social referencing occurs in wild chimpanzees when an unhabituated adult female chimpanzee enters a habituated group and rapidly becomes habituated based on her conspecifics' behaviour. Accordingly, social referencing may continue through adulthood, given the high adaptive value of social referencing.

Behavioural regulation

There was little evidence for behavioural regulation based on information received in the orang-utans either for naturally occurring events, or in

response to long calls. Both mothers responded fearfully to Allen's long call and immediately picked up their offspring without initial reference to conspecifics. The orang-utans' affect was best described as vigilant during playback vocalisations. Upon hearing the vocalisation, individuals sat up, ceased any ongoing activities, and remained motionless whilst alternating attention between the location of the vocalisation and a conspecific. If individuals withdrew or changed position, referencing occurred after movement rather than before.

Methodological issues

This is the first study to investigate social referencing in orang-utans within a social environment, in response to naturally occurring events and playback vocalisations. There is little documentation of baseline levels of social referencing, occurring in the absence of stimuli or in response to familiar stimuli (Baldwin & Moses, 1996). Few studies (even in human infants) have been conducted in non-experimental situations. For orang-utans, familiarity influenced whether an event was visually attended, and biological relevance influenced social referencing behaviour. In an un-manipulated situation (study 1) seeking information from conspecifics appeared restricted to younger individuals. However, playback vocalisations of long calls induced referential looking in all orang-utans.

The main difference between this study and traditional studies of social referencing was the object of reference. Because no physical object was present and events generally occurred outside the exhibit, orang-utan physical responses may not be comparable to those observed in usual social

referencing studies. The orang-utans could not approach and touch the event, actions which may be important for behavioural regulation. However, in order to study social referencing within the natural environment and gain a baseline measure of referencing behaviour (orang-utans observed in their outdoor exhibits and in their natural groups), it was considered important to conduct the study using non-invasive and biologically relevant stimuli.

Can social monitoring be used to gain social information?

The data from this study indicated that social looks towards conspecifics increased post-playback period, as did referential looks. As observed in infant chimpanzees by Russell et al. (1997), when orang-utan social looking occurred, most looks were immediately followed or preceded by looks to the vocalisation location. Roberts et al. (2008) reported increased social monitoring in wild Barbary macaques in the presence of toy snake. However, only two out of 15 infant macaques engaged in referential looking (Roberts et al., 2008). This questions whether alternation of gaze is necessary for receiving and acting upon information received from conspecifics. Gaze alternation is viewed as a solicitation for information (Russell et al., 1997) and a sign of intentionality in communication involving a social agent to achieve an objective (Chadwick-Jones, 2000). Therefore, the propensity to alternate gaze has important implications for understanding the cognitive aspects of social referencing. Social monitoring provides important information on conspecifics' behaviour (Dunbar, 1988). However, the alternation of gaze indicates an active request for information. Consideration of why an individual is monitored, what information is gained and how that

might influence or change behavioural responses would help elucidate the communicative and information seeking aspects of visual attention.

Conclusions

This study has two implications for future research. In a captive environment, social referencing is a rare event. This study suggests that naturally occurring events are appraised individually based on familiarity and biological relevance. Whether this pertains to orang-utans as a species, orang-utans at Zoo Atlanta or any captive groups of primates is unknown given the lack of information on naturalistic referencing in either adult humans or primates. Secondly, social referencing in both adult and young orang-utans occurs reliably in response to long call vocalisations even in a captive setting. This suggests that the propensity to seek social information is a developmental process that is likely to continue into adulthood.

Given the success of eliciting social referencing with long call playbacks, this design offers significant promise for future research. Clearly, more examples and more observations are needed to determine the effect of familiarity or ambiguity on social referencing in zoo housed orang-utans.

CHAPTER 7

A UNIFYING EXPLANATION FOR SOCIAL MONITORING AND ITS ROLE WITH VIGILANCE IN PRIMATE GROUPS

Overview

In this chapter, I reconcile the social monitoring data collected from five species of primates in the previous chapters. The first study in this chapter considers social monitoring within an overall visual budget framework, to evaluate how these species of primates allocate their visual time. The influence of context and attention types are addressed to evaluate the portioning of attention to social and non-social targets. The second study in this chapter uses important social variables (identified in the previous chapters) to determine if: a) the frequency of social monitoring can be predicted from these variables and b) whether these social predictor variables are relevant for different contexts.

I collect evidence for a unifying view of social monitoring within an overall vigilance framework to understand why social monitoring is more complex and multi-faceted than previously considered.

Introduction

As discussed in the introductory chapter, visual attention in primates is typically studied from two perspectives: one emphasising an anti-predatory function of visual attention (attention directed outside the group) and one emphasising a social function of visual attention (based on avoidance of aggression or competition within the group). Both of these approaches focus on threat protection or competition in shaping patterns of attention. This means that, usually, visual attention is considered as threat-related vigilance regardless of the target of attention.

Portioning attention to social and non-social targets

Social and non-social monitoring are assumed to be mutually exclusive. That is, if attention is directed away from the social group it cannot be directed simultaneously towards the social group. However, monitoring conspecifics within the same social group might serve two functions: providing an early warning about predators through alert postures of conspecifics (Treves, 2000) and providing important information about conspecifics' behaviour (Dunbar, 1988). Current knowledge on vigilance is difficult to reconcile when studies on visual attention either focus solely on social monitoring; solely on non-social monitoring (towards predators or extra-group troops); or do not specify the target of visual attention.

Vigilance is costly (i.e. active scanning of the environment), both in terms of time and proportion of attention allocated, yet little is known about how vigilance compares to other types of visual attention. Some of these costs can be offset by living in larger groups, since individuals can benefit

from collective vigilance among associates. However, there is no conclusive evidence that vigilance decreases in larger groups (Treves, 1997; 1998a; 2000; Treves et al., 2001). Consequently, Treves (1999) has argued that as group size increases, social monitoring increases. The total level of vigilance remains similar across groups but it is the proportion of vigilance directed towards conspecifics that changes in larger groups (thus accounting for the absence of a group size effect). However, only weak support has been found for the group size component of this theory (Treves, 1999; Treves & Baguma, 2002). Instead, social organisation and the level of competition are believed to influence how vigilance is portioned to social and non-social targets.

Does competition influence allocation of attention?

Caine and Marra (1988) reported that although both squirrel and tamarin monkeys were equally vigilant during feeding, squirrel monkeys spent a greater portion of visual time monitoring conspecifics, while tamarins devoted most of their visual attention towards the non-social environment. The attentional demands associated with being part of a group characterised by dominance relationships and agonistic tension may have accounted for squirrel monkeys allocating roughly half their vigilance to monitoring conspecifics and the remaining half monitoring the non-social environment. In contrast, because tamarins lack this social excitability, roughly 80% of tamarins' attention was directed to the environment in the absence of these social demands (Caine & Marra, 1988). Pannozzo et al. (2007) reported that high-ranking capuchin monkeys apportioned more vigilance to the non-social

environment than conspecifics while subordinate individuals allocated more attention towards conspecifics.

These findings suggest that although intra-group competition and social organisation may not influence how vigilant an animal is (i.e. the number of times the head is moved), it may influence the proportion of visual time allocated to conspecifics compared to non-social targets. Comparing the amount of visual time allocated for non-social targets to visual time for social targets puts the social monitoring data into a broader perspective examining the social influences on the targeting of visual attention.

The influence of context on visual attention

As reviewed in chapter 1, numerous studies indicate that attentionally demanding activities such as feeding and grooming are incompatible with vigilance. However, when social attention is considered, social monitoring may occur at a higher rate during feeding compared to resting (Treves & Baguma, 2002); in a food competitive context compared to a non-food context (Blois-Heulin & Girona, 1999), or when food is clumped rather than dispersed (Blois-Heulin & Martinez-Cruz, 2005).

Therefore, comparing social and non-social attention in different contexts addresses two questions. First, whether the portioning of visual attention towards targets is influenced by context. Second, unlike general vigilance, whether social monitoring increases and non-social monitoring decreases in feeding contexts due to increased competition within the group.

Attention types and context

A visual response to food competition (Blois-Heulin & Girona, 1999) and nervousness (Mitchell, 1972) is thought be the use of rapid glances. In the presence of preferred food, glances occur more frequently and particularly by subordinates (Blois-Heulin, 1999; Blois-Heulin & Girona, 1999). In the absence of food and competition, looks (a longer duration of attention) may be used more frequently than glances (Blois-Heulin & Girona, 1999). However, it is unclear whether glances and looks are specific to social monitoring and whether non-social attention occurs at a lower rate during food contexts compared to resting. The use of glances during feeding are likely to be linked to the attentional demands associated with feeding. Feeding may necessitate the use of glances, rather than glances being used in response to social competition.

The previous chapters in this thesis examined the underlying basis of social monitoring in different species of primates, showing that dyadic relationship quality was an important variable that was consistently overlooked by previous studies of social monitoring. The goal of this chapter is to evaluate social monitoring from a wider visual budget perspective, encompassing the use of glances and looks, context, and targets of attention, to assess how much relative time from the visual budget is allocated towards monitoring conspecifics.

STUDY 1: TESTING A MULTI-FACETED STRUCTURE OF VIGILANCE

Specific predictions were made to test a multi-faceted structure of vigilance based on competition and attentional demands, accounting for species, context, attention type and the targets of vigilance.

i) Vigilance is influenced by context and attention types.
   a) Glances may be used to permit an individual to be briefly vigilant without interrupting an activity. Therefore, both social and non-social glances will occur more frequently during feeding context compared to resting context.
   b) Looks are frequently used when there are fewer demands on visual attention. Therefore, both social and non-social looks would occur more frequently during resting context compared to feeding context.

ii) Social and non-social monitoring are influenced similarly by context and attention type.
   a) Social and non-social monitoring are subject to the same constraints on visual attention. Therefore, glances and looks to social and non-social targets should occur equally during feeding.

iii) However, if social monitoring reflects competition, then:
   a) More social glances than non-social glances occur during feeding.
   b) More social looks occur during feeding than non-social looks.

Methods

Data collection

The data collection protocols for social behaviour and visual attention are detailed in chapter 2. In this study, all categories of visual attention were used to construct a visual budget for each species. Additionally, visual attention was considered across all contexts, and then specifically during feeding and resting contexts. The type of attention i.e. glances and looks used were considered further.

Data analysis

Univariate ANOVA's with adjusted pairwise comparisons were employed to identify species differences in visual budgets. A multifactor mixed ANOVA was conducted to evaluate the role of context, attention type and targets of attention as a function of species (species x feeding/resting context x social/non-social target x glance/look). These analyses used rates of attention. Percent of visual time in attention states is presented descriptively.

Results

Visual attention budgets

Visual budgets varied with species (Table 7.1). Species differed in time spent in passive attention: $F(5,77) = 25.210$, $p = <0.001$; occupied attention: $F(5,77) = 25.421$, $p = <0.001$; and time spent vigilant (all monitoring): $F(5,77) = 14.222$, $p = <0.001$. All the species differences in visual budgets pertained to the orang-utans and baboons (pairwise comparisons).

Table 7.1 Visual budgets: percent visual time spent in each attention state.

	Unknown	Passive	Occupied	Vigilance	
				Social	Non-social
Chimpanzees	0.4	30.1	39.1	9.8	20.7
Siamangs	0.4	25.9	37.8	12.1	23.8
Orang-utans	4.4	36.7	36.2	4.1	18.4
Lemur Birth	2.0	28.6	36.4	8.8	24.2
Lemur Mating	0.9	30.2	32.4	11.4	25.1
Baboons	0.2	19.4	54.3	17.2	8.6
Mean	1.4	27.1	42.5	11.6	17.3
SD	3.2	8.2	11.5	5.3	8.6

Orang-utans spent more time in passive attention compared to siamangs, birth season lemurs and baboons. Approximately 54% of visual attention in baboons was occupied, which was significantly more than the other species. While orang-utans were less vigilant than the chimpanzees, siamangs, and lemurs; and baboons less vigilant than siamangs and lemurs; different trends were evident when social targets of vigilance were considered: $F(5,77) = 89.603$, $p = <0.001$. Orang-utans monitored conspecifics less frequently than the other species, whereas baboons monitored conspecifics more frequently than all the other species.

Vigilance as a function of context

Vigilance varied according to context (Table 7.2). Vigilance was reduced during feeding context compared to resting context and this applied to social and non-social monitoring. However, the mean difference between social and non-social monitoring was much greater in the resting context. Non-social monitoring almost doubled when the context changed from feeding to

resting. While social monitoring increased somewhat during resting context, it did not increase as much as non-social monitoring did.

Table 7.2 Percent of visual budget allocated to vigilance in feeding and resting contexts.

	Feeding context			Resting context		
	Total vigilance	Non-social	Social	Total vigilance	Non-social	Social
Chimpanzees	28.2	16.8	11.4	43.2	30	13.2
Siamangs	30.4	19.6	10.8	45.9	31.2	14.7
Orang-utans	20.5	16.4	4.1	35.0	30	5.0
Lemur Birth	18.4	13.7	4.7	48.4	35.7	12.6
Lemur Mating	23.9	16.8	7.2	52.6	36.3	16.3
Baboons	25.6	7.9	17.7	31.2	11.5	19.7
Mean	24.5	15.2	9.3	42.7	29.1	13.6

If visual attention types are used differently according to context, target and by species, then this may account for the patterns observed in Table 7.2; this was explored further using an analysis of variance.

The interaction of species, context, attention type and target on visual attention

All main effects and interactions of the ANOVA were significant, including the four-way interaction: $F(5,77) = 14.815$, $p = <0.001$. Therefore, the influence of context, attention type, target, and species depended on the levels of the other factors. Accordingly, the lower-order interactions were not analysed in favour of decomposing the four-way interaction.

Is there an interaction between context, attention type and target for all species?

Initially, the three-way interaction was considered for each species separately. The interaction of context, attention type, and the target of attention was significant for all species: chimpanzees: $F(1,5) = 26.343$, $p = 0.004$; siamangs: $F(1,3) = 19.007$, $p = 0.022$; orang-utans: $F(1,15) = 5.505$, $p = 0.033$; birth season lemurs: $F(1,13) = 108.089$, $p = <0.001$; mating season lemurs: $F(1,12) = 280.544$, $p = <0.001$; baboons: $F(1,29) = 16.030$, $p <0.001$. To understand and picture these significant effects, the three-way interaction was broken down to influences of context and attention type at each level of target.

Does social monitoring vary as a function of attention types and context?

There was an interaction of context and attention type on social monitoring for all species apart from the orang-utans: $F(1,15) = 0.923$, $p = 0.352$, indicating that the orang-utans' use of social looks and glances did not change between contexts. However, there was a significant interaction for chimpanzees: $F(1,5) = 50.584$, $p = 0.001$; siamangs: $F(1,3) = 23.754$, $p = 0.017$; birth season lemurs: $F(1,13) = 278.130$, $p = <0.001$; mating season lemurs: $F(1,12) = 123.079$, $p = <0.001$; and baboons: $F(1,29) = 190.436$, $p <0.001$ (Figure 7.1).

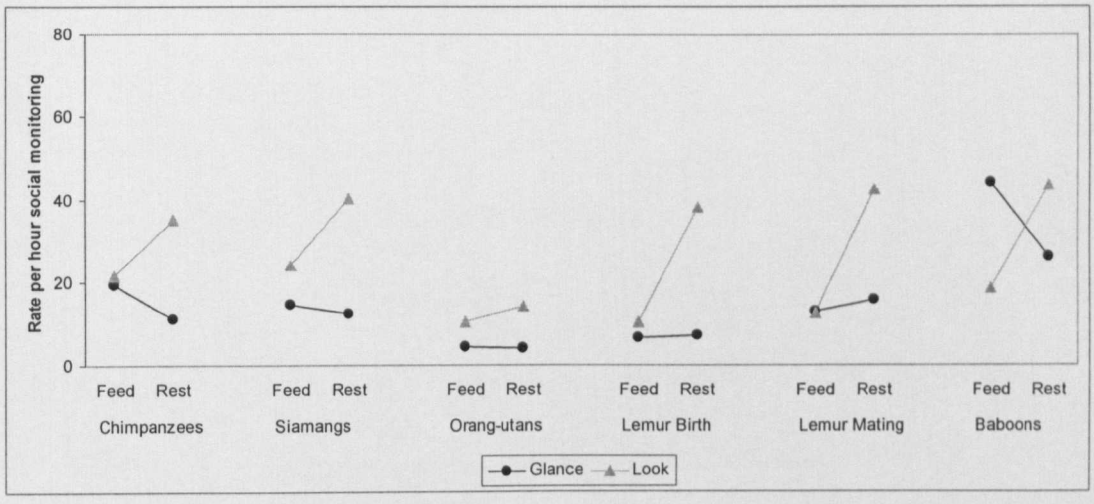

Figure 7.1 The interaction of context and attention type on social monitoring.

Social looks

The significant interaction of context and attention type on social monitoring for all species (apart from the orang-utans) was primarily attributable to the significantly higher rate of social looks in the resting context compared to the feeding context: chimpanzees: $t(5) = -8.344$, $p = <0.001$; siamangs: $t(3) = -3.912$, $p = 0.030$; birth season lemurs: $t(13) = -14.103$, $p <0.001$; mating season lemurs: $t(12) = -15.270$, $p = <0.001$; baboons: $t(29) = -10.151$, $p = <0.001$.

Social glances

The species showed more variability on the use of social glances between the contexts. For chimpanzees and baboons, the use of social glances decreased significantly from feeding context to resting context: chimpanzees: $t(5) = 5.985$, $p = 0.002$; baboons: $t(29) = 8.686$, $p = <0.001$ The other species used glances equally between the contexts: birth season lemurs: $t(13) = -$

0.665, p = 0.518; mating season lemurs: t(12) = -2.228, p = 0.046; siamangs: t(3) = 1.552, p = 0.219; orang-utans: t(15) = 0.225, p = 0.825.

Does non-social monitoring vary as a function of attention type and context?

There was an interaction of context and attention type on non-social monitoring for all species: chimpanzees: F(1,5) = 96.680, p = <0.001; siamangs: F(1,3) = 131.993, p = 0.001; orang-utans: F(1,15) = 8.991, p = 0.009; birth season lemurs: F(1,13) = 359.049, P = <0.001; mating season lemurs: F(1,12) = 677.571, p = <0.001; baboons: F(1,29) = 107.279, p = <0.001 (Figure 7.2).

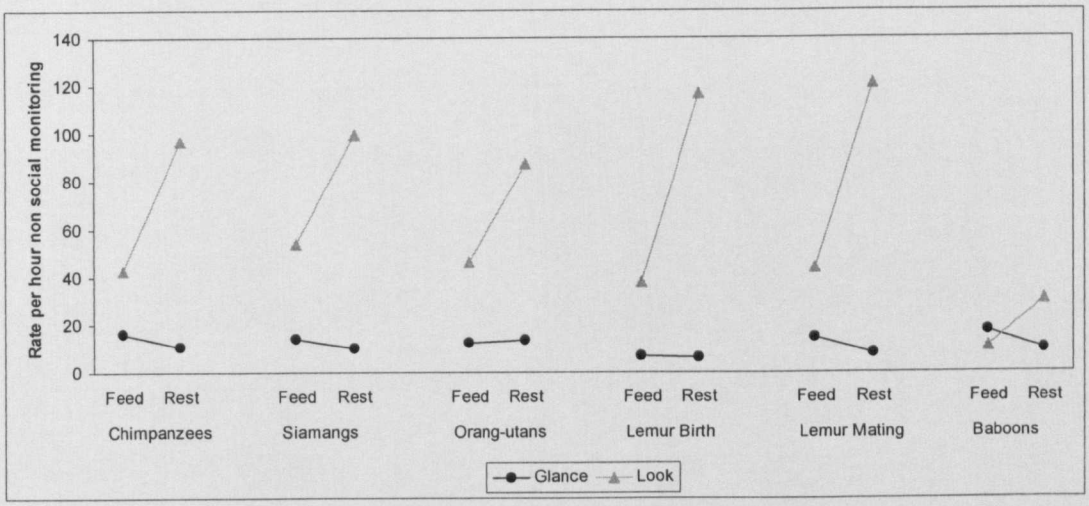

Figure 7.2 The interaction of context and attention type on non-social monitoring.

Non-social looks

As observed for social looks, the interaction between context and attention type for non-social looks was significant for all species. This was because all species increased non-social looks from feeding context compared to resting

context: chimpanzees: $t(5) = -9.660$, $p = <0.001$; siamangs: $t(3) = -10.223$, $p = 0.002$; orang-utans: $t(15) = -3.044$, $p = 0.008$; birth season lemurs: $t(13) = -19.176$, $p <0.001$; mating season lemurs: $t(12) = -23.517$, $p = <0.001$; baboons: $t(29) = -8.278$, $p = <0.001$.

Non-social glances

As observed for social glances, species differences were evident. Non-social glances in chimpanzees, baboons and mating season lemurs were significantly reduced when the context changed from feeding to resting. Chimpanzees: $t(5) = 3.011$, $p = 0.030$; baboons: $t(29) = 7.160$, $p = <0.001$; mating season lemurs: $t(12) = 5.873$, $p = <0.001$. However, siamangs: $t(3) = 1.672$, $p = 0.193$; orang-utans: $t(15) = -0.255$, $p = 0.802$; and birth season lemurs: $t(13) = 0.738$, $p = 0.474$ engaged in similar rates of non-social glances in both contexts.

Are social targets monitored more than non-social targets as a function of context and attention type?

Because simple main effects at the level of context have already been interpreted for the frequency of attention between species; social and non-social monitoring for each species were interpreted for each context separately (see Table 7.3 for a summary).

Feeding context

Glances. For the majority of species, social and non-social glances were used equally during feeding context: chimpanzees: $t(5) = -1.366$, $p = 0.230$;

siamangs: t(3) = -0.357, p = 0.744; birth season lemurs: t(13) = 0.163, p = 0.873; mating season lemurs: t(12) = 1.634, p = 0.128. However, baboons glanced more frequently at social targets compared to non-social targets: t(29) = -24.02, p = <0.001 while orang-utans glanced at non-social targets more frequently than social targets: t(15) = 3.491, p = 0.003.

Looks. During feeding context, all species except baboons looked more frequently at non-social than social targets: chimpanzees: t(5) = 4.497, p = 0.006; siamangs: t(3) = 5.196, p = 0.014; orang-utans: t(15) = 3.475, p = 0.003; birth season lemurs: t(13) = 10.110, p = <0.001; mating season lemurs: t(12) = 9.848, p = <0.001. Baboons looked more at social than non-social targets : t(29) = -6.409, p = <0.001.

Resting context

Glances. Generally, glances were used to monitor both social and non-social targets equally: This applied to chimpanzees: t(5) = -2.499 p = 0.055; siamangs: t(3) = -0.935, p = 0.423; orang-utans: t(15) = 1.969, p = 0.068; and birth season lemurs: t(13) = -1.169, p = 0.263. However, both mating season lemurs: t(12) = -6.141, p = <0.001 and baboons: t(29) = -8.142, p = <0.001 used significantly more social glances than non-social glances during resting context.

Looks. During resting context, all species except baboons used looks to monitor non-social targets more frequently than social targets: chimpanzees: t(5) = 7.933, p = <0.001; siamangs: t(3) = 4.745, p = 0.018; orang-utans:

t(15) = 4.760, p = <0.001; birth season lemurs: t(13) = 13.047, p = <0.001; mating season lemurs: t(12) = 21.097, p = <0.001. Baboons looked more frequently at social than non-social targets: t(29) = -4.146, p = <0.001.

Table 7.3 Non-social and social monitoring as a function of context and attention type.

Context	Glances			Looks		
	NS = Soc	Soc > NS	NS > Soc	NS = Soc	Soc > NS	NS > Soc
Feeding	C S LB LM	B	O		B	C S O LB LM
Resting	C S O LB	B LM			B	C S O LB LM

NS=Soc denotes non-social and social monitoring occur at an equal rate
NS > Soc or Soc > NS denotes social monitoring occurred at a different rate than non-social
C, S, O, LB, LM, B denote the first letter of the species

Discussion

The results of study 1 highlight that vigilance is influenced by a number of factors. Firstly, visual attention budgets varied by species and by context. Visual budgets are important because they address the visual attention that does not relate to social monitoring and other visual demands that might facilitate or hinder social monitoring. For instance, increased passive attention (orang-utans) and increased occupied attention (baboons) meant that less visual time was available to be vigilant. Importantly, the targets of vigilance confirm that it is necessary to consider the portioning of vigilance to social and non-social targets.

Both social and non-social monitoring were influenced by context, and consequently attention type, with these influences varying by species. While decreased vigilance is often reported during feeding, in this study only looks (both social and non-social) decreased during feeding. Glances appeared to permit an individual to remain vigilant while feeding. Chimpanzees and baboons used both social and non-social glances significantly more often during feeding context compared to resting context. There was little evidence to support suggestions that social glances are responsive to competition during feeding (Blois-Heulin & Girona, 1999). This was because, within the feeding context, social and non-social glances were used equally (with the exception of baboons and orang-utans).

The study confirms that social monitoring, like non-social monitoring, is influenced by context, and that attention types are not restricted to particular targets e.g. glances are used to monitor both conspecifics and the environment. Nonetheless, the visual budget emphasises the need to separate social from non-social monitoring in order to gain an accurate picture of vigilance in primates.

STUDY 2: MULTIPLE REGRESSION ANALYSIS OF SOCIAL MONITORING

Given the variability in vigilance as a function of context and species, further analyses of social monitoring were undertaken. A hierarchical multiple regression analysis was conducted specifically for social monitoring in study 2. The objective was to expand on the variables that have been identified as important for social monitoring throughout the chapters. The aim of this final

study is to identify and quantify specific social behaviours that influence rates of social monitoring in the study species. Can a statistical model of social monitoring be applied to different contexts to account for the variability of social monitoring observed between species? Although social influences on attention have been emphasised throughout this thesis, do social variables really account for a significant proportion of variance in social monitoring? I attempt to reconcile some final issues of social monitoring to evaluate why some primates monitor more frequently than others.

Methods

Data analysis

A hierarchical multiple regression of social monitoring was conducted. Here, variables perceived to influence social monitoring were entered into the regression equation first. Group size was used as a proxy for species, because variability in social monitoring was expected to be related to species differences as a function of the number of individuals available to monitor within the group. In order to test the attention structure theory (Chance, 1967; Chance & Jolly, 1970) and its emphasis on competitive influences on social monitoring, the rate of aggression received, the sex of the animal and the presence of a rank hierarchy were entered second. The third step involved entering the rate of affiliative behaviours and proximity (the percent of time individuals had a nearest neighbour within five metres). Interaction terms with group size (group size x affiliation, group size x aggression received, group size x proximity and group size x sex) were entered in the fourth and final step. The fact that the larger groups in this sample

possessed a rank based social structure precluded a group size x rank interaction term.

Results

Social monitoring across all contexts

The results of the regression analysis are presented in Table 7.4. The overall F test indicated that R^2 was significantly different from zero at the end of each step and after step 4, with all variables in the equation: F (10,72) = 50.342, p = <0.001. Adjusted R^2 was 0.85, indicating that 85% of the variation in social monitoring could be accounted for by a regression equation using the estimates of 10 variables.

Table 7.4 Regression model of overall social monitoring.

Step	Final model	R^2 change	B	SE B	β
	Constant		41.976	7.483	
1	Group size	0.711**	0.442	0.076	.582**
2	Aggression received	0.063**	1.713	0.522	.159*
	Sex		3.449	1.825	.088
	Rank		-1.964	3.883	-.044
3	Affiliation	0.053**	0.230	0.365	.055
	Proximity		0.206	0.105	.247[a]
4	Group x affiliation	0.047**	-0.021	0.017	-.113
	Group x proximity		0.002	0.004	.045
	Group x aggression		-0.051	0.023	-.111*
	Group x sex		0.248	0.076	.204*

*p<0.05; **p <0.001; [a] p = 0.06

The estimates of β for group size and aggression received were significant, indicating these two variables were the most useful predictors in accounting for unique variation in overall rates of social monitoring. However, the significant interaction term between these two variables indicated that the influence of aggression received on social monitoring was moderated by group size (Figure 7.3). When received aggression was high, individuals in large and small groups monitored relatively equally. However, when received aggression was low, individuals in large groups monitored more frequently than small groups. The group size and sex interaction term indicated that male and female social monitoring was equal in small groups, but males monitored more frequently than females in large groups.

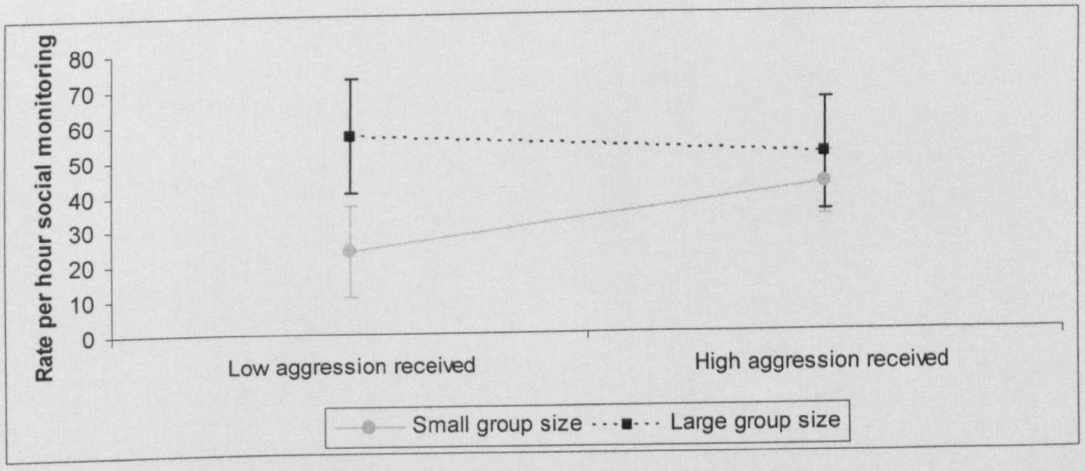

Figure 7.3 Social monitoring as a function of group size and aggression received.

Applying the regression model to social monitoring in feeding and resting contexts

Study 1 indicated that social monitoring varied according to the context in which it occurred and so the regression model was used to ascertain the

best fitting model first for the feeding context, then for the resting context. If both models were similar in terms of variance accounted for in each step and the contribution of each variable, then this would argue against the differential role of context in determining social monitoring.

Feeding context

For the model specifying social monitoring in the feeding context, a three-step model without the interaction terms was the best fitting model: $F(6,76) = 56.003$, $p < 0.001$ (Table 7.5). Using the three-step model, 81% of the variance in social monitoring could be accounted by six predictors. Specifically, although individuals in larger groups monitored more frequently during feeding, individuals that engaged in affiliative behaviours monitored more frequently also. Importantly, in the feeding context, neither aggression received or sex were important predictors for social monitoring. The interaction terms did not contribute to a significant R^2 change.

Table 7.5 Regression model for feeding context social monitoring.

Step	Final model	R^2 change	B	SE B	β
	Constant		40.400	4.002	
1	Group size	0.742**	0.8376	0.057	.934**
2	Aggression received	0.005	0.395	0.680	.032
	Sex		1.727	2.262	.038
	Rank		-4.646	4.918	-.089
3	Affiliation	0.068**	1.246	0.318	.258*
	Proximity		0.017	0.101	.017

*p<0.05; **p <0.001

Resting context

The best fitting regression of resting context social monitoring consisted of all four steps. Specifically, 69% of the variance in social monitoring was accounted by the final model: $F(10,72) = 19.486$, $p = <0.001$ (Table 7.6).

Table 7.6 Regression model for resting context social monitoring.

Step	Final model	R^2 change	B	SE B	β
	Constant		50.806	13.669	
1	Group size	0.440**	0.410	0.138	.431*
2	Aggression received	0.132**	0.595	0.957	.045
	Sex		3.970	3.333	.083
	Rank		2.900	7.092	.052
3	Affiliation	0.070*	0.398	0.666	.078
	Proximity		0.237	0.192	.229
4	Group x affiliation	0.088**	-0.010	0.031	-.046
	Group x proximity		-0.002	0.008	-.034
	Group x aggression		-0.164	0.042	-.284**
	Group x sex		0.215	0.139	.140

*p<0.05; **p <0.001

While the variance accounted for was similar in the resting context model to that obtained in the overall model, the influence of the individual predictors differed in the resting context model. In the overall model, group size and the interaction term of group size with aggression received were significant predictors of social monitoring. In the resting context, group size only accounted for 44% of the variance (not over 70% as in the feeding and overall contexts). The interaction of group size and aggression received was similar to that in the overall model (comparing Figure 7.3 with 7.4), however,

in the resting context there was more overlap between large and small groups when aggression received was high. Additionally, the increase in social monitoring in large groups when received aggression was low, was a steeper increase than that observed in the overall model.

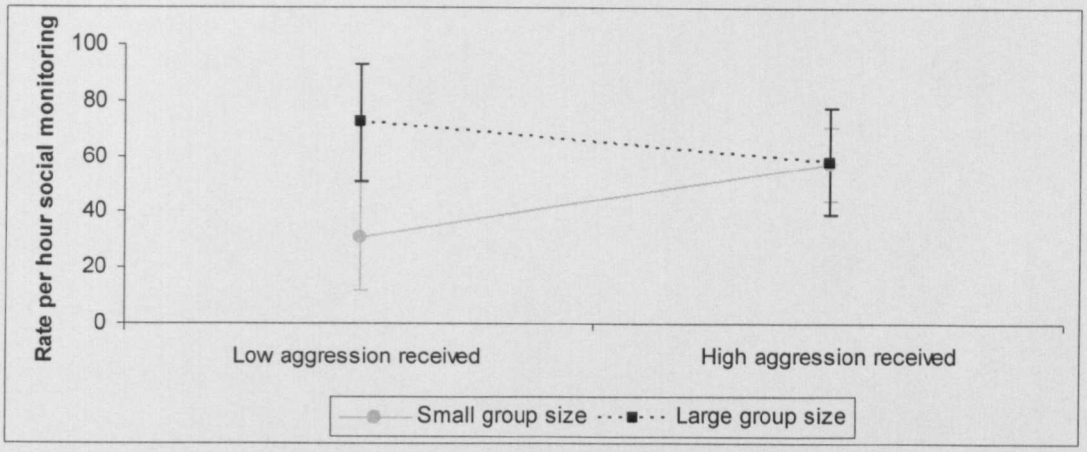

Figure 7.4 Social monitoring during resting context as a function of group size and aggression received.

General Discussion

Studies 1 and 2 compared visual attention across multiple primate species contributing to and extending current knowledge on social monitoring. Firstly, visual time available to monitor conspecifics varies as a function of existing demands on attention. Secondly, the influence of specific social variables on social monitoring e.g. aggression received, differs according to additional attributes such as context and group size.

The results in the first study indicated that within five species of primates, overall visual attention budgets were rather homogenous. Roughly, one third of visual time was spent occupied, one third in passive attention and one third spent vigilant. Importantly, the species differed in patterns of

vigilance when target, attention type and context were considered. The second study presented statistical support for differential predictors of social monitoring as a function of context and social variables. In addition to group size, social behaviours accounted for a significant proportion of variance in the frequency of social monitoring across different contexts.

A multi-faceted basis of visual attention

Context and competition

The data support studies indicating a reduction in vigilance during attentionally demanding activities such as feeding (Kutsukake, 2006; Hill & Cowlishaw, 2002; Hirsch, 2002; Treves, 2000; Treves et al., 2001; Uhde & Sommer, 2002; van Schaik & van Noordwijk, 1989). Additionally, both social and non-social monitoring were reduced during feeding context.

Although species differences existed concerning the frequency of visual attention, the overall patterning of attention was consistent. For instance, all species increased social and non-social looks in the resting context compared to the feeding context. More species variation was evident when considering the use of glances. Blois-Heulin & Girona (1999) suggested that social glances are indicative of the level of competition within primate groups. The problem with this competition interpretation of glances is that it is difficult to confirm whether social glances are associated with competition, or associated with the attentional demands required for feeding when there are no data available on non-social attention as well. Comparison of data from non-competitive, attentionally demanding contexts, such as

grooming or self-directed behaviour, would further elucidate the role of glances in reflecting existing attentional demands.

The data in this study are more consistent with the interpretation that glances reflect existing attentional demands e.g. feeding and/or species differences. Both social and non-social looks were consistently more frequent in resting context compared to feeding context for all species, supporting an influence of context on the deployment of looks. Overall, the findings suggest that looks more than glances are influenced by context, and glances characterised by more species variability. While the use of looks is associated with decreased competition (Blois-Heulin & Girona, 1999), looks rather than glances are the most frequent attention type (Blois-Heulin & Girona, 1999; Blois-Heulin & Martinez-Cruz, 2005). Thus the reduction of both social and non-social looks during feeding, would account for decreased overall vigilance during feeding reported in previous studies (e.g. van Schaik & van Noordwijk, 1989).

In the current study, five species of primates were studied, all with contrasting social organisations and group compositions, yet similar patterns of attention were evident. Therefore, it seems unlikely that the consistency of looking can be reduced to a simple lack of competition, equally applicable to all species. Instead, it seems more appropriate to consider that looks, by definition, occupy more visual time; therefore when attention is compromised e.g. during feeding, looks would be reduced. The glance data however, are difficult to reconcile into an attentional demands framework. It was hypothesised that glances are responsive to context: if attention is occupied, then glances may be used in order to remain vigilant without ceasing an

activity for too long. The influence of context on use of glances appears to also vary by species, as some of the species used glances equally in feeding and resting contexts. However, for chimpanzees, mating season lemurs and baboons, competition within the group may be high (chapters 3 and 4). Additionally, more individuals to monitor may result in glances being utilised more frequently. In this case, attentional demands - not as a result of context, but from living in large, dynamic groups, may have accounted for the results obtained.

Why group size is important for comparative social monitoring studies

The data from study 1 highlighted differences in visual attention budgets particularly in baboons and orang-utans compared to the other species. Most orang-utans' attention was directed towards non-social targets, while baboons directed attention primarily to social targets. These findings may simply indicate that more potential targets of attention in a large baboon group places increased demands on visual attention. This seems likely given that baboons also used social glances during resting context. These social demands are in addition to attentional demands associated with activities such as feeding. Therefore, rapid monitoring (glances rather than looks) may facilitate vigilance when vigilance would otherwise be difficult. Accordingly, living in a larger or a more dynamic social group with strong social relationships might be considered as attentionally demanding due to a greater number of potential targets to monitor, and consequently more 'attention getting' social events taking place. The data from the baboons suggest this may be the case.

Study 2 confirmed that group size was indeed of primary importance for social monitoring. Group size accounted for a large and significant proportion of variance in social monitoring. This could be interpreted in terms of increased competition existing in larger groups (Treves, 1999). However, affiliation, not aggression, accounted for a significant proportion of variance once group size was accounted for in the model of feeding context social monitoring. Secondly, in the overall and resting context models, the influence of group size on social monitoring varied as a function of aggression received. Individuals in larger groups engaged in more social monitoring when received aggression was low, but decreased social monitoring when aggression was high.

Group size also interacted with sex: males in larger groups monitored more frequently than females. Male-male competition is high in mating season lemurs (e.g. Jolly, 1966; Parga, 2006; Sauther, 1991; chapter 3) and in baboons (Smuts, 1985; chapter 4), both of which reside in larger groups. Competition is by no means associated with the group as a whole, but based on dyadic relationships. Indeed, increased monitoring by male lemurs and baboons is unlikely to be solely associated with competitive influences, given males from both species also showed monitoring of female friends. When there are more individuals in the group, monitoring may be frequent due to keeping track of a large number of both friends and adversaries (Dunbar, 1988).

Social variables explain variability in frequencies of social monitoring

Aggression. Based on the attention structure theory (Chance, 1967; Chance & Jolly, 1970) one may expect social monitoring to be more rigid in groups with rank order, and increase with the level of aggression received. The attention structure was not fully supported in this study. Rank was not a significant predictor of social monitoring, and effects of aggression received on social monitoring were moderated by group size. Social monitoring was most frequent in larger groups but decreased when aggression received was less frequent. However, individuals in smaller groups showed increased rates of monitoring when rates of aggression received increased, overall and during the resting context.

If social monitoring is influenced by group size and received aggression, then this may account for the positive results of aggression received on social monitoring documented in past studies (chapter 1), as groups in social monitoring research typically consist of fewer than eight individuals. In larger groups, social monitoring may function in the avoidance of aggression i.e. when there are more adversaries to avoid. This is supported by the fact that individuals in large groups that engaged in higher rates of social monitoring received lower rates of aggression. Conspecific aggression has high reproductive and fitness costs (Sussman et al., 2005; Treves, 2000), and the easiest way to minimize agonism may be to avoid it by visually monitoring and anticipating the behaviour of conspecifics.

Affiliation. For the feeding context model of social monitoring, affiliation and group size were the most important predictors. That is, individuals that

engaged in more friendly interactions (as initiator or recipient) monitored conspecifics more frequently during feeding. In the overall model, there was a trend concerning proximity, indicating solitary individuals monitored conspecifics less frequently. The presence of nearest neighbours can increase vigilance (Hirsch, 2002; Kutsukake, 2006; 2007); alternatively, peripheral individuals may be more vigilant (Hill & Cowlishaw, 2002; Treves et al., 2001). Since these studies did not identify the targets of vigilance, one cannot be sure whether a cohesion effect applies to social monitoring specifically rather than all vigilance. The current study suggests that cohesion is not a strong predictor of social monitoring.

Feeding has been associated with increased competition and increased social monitoring (Blois-Heulin, 1999; Blois-Heulin & Girona, 1999; Blois-Heulin & Martinez-Cruz, 2005; Treves & Baguma, 2002). However, in Caine & Marra's (1988) study, presentation of additional food trays (presumably to reduce competition) resulted in greater social monitoring in squirrel monkeys. Therefore, the role of social monitoring during feeding may be highly variable. In the current study, the finding that more affiliative individuals engaged in higher rates of social monitoring during feeding suggests a potential role of keeping track of affiliates. Monitoring friends during feeding may be important to ensure an ally is near in case aggression occurs. During clumped feeding times, captive chimpanzees increase proximity with preferred grooming partners, possibly as an attempt to increase tolerance to facilitate co-feeding (Koyama, 2000). Additionally, having affiliates close to hand may also help in gaining access to resources.

This is an interesting possibility, and evaluation of nearest neighbours would aid interpretation of the role of social monitoring plays during feeding.

What we now know about social monitoring and where to go next

Social monitoring is a highly variable behaviour that is responsive to affiliation, aggression, sex, season, proximity and species. The results of this chapter highlight the importance of breaking down vigilance into two mutually exclusive types: attention to non-social targets and attention to social targets. Moreover, it is vital to identify multiple behavioural indicators to explain the frequency of social monitoring and of non-social monitoring in primate groups.

This study indicates that group size is important for social monitoring, when comparing the frequencies of monitoring between species. It is not clear however, if baboons engaged in the highest rates of social monitoring because of their group size, or other variables associated with large group size e.g. social complexity, or due to some characteristic of the species. If group sizes are representative of the species in question, can social monitoring be compared between species if some species simply have more individuals to attend visually? Treves and Baguma (2002) argue against using data corrected for the availability of associates as it eliminates inter-species differences. Their study found the lowest rates of monitoring in howler monkeys with a typical group size of 10 compared to larger groups of guenons and colobus monkeys. Even in larger groups, not every individual is monitored equally; the salience of some individuals over others has been well documented in the previous chapters. The baboon data suggest that

although a larger group size may contribute to increased social monitoring in this species, it is likely that monitoring is also important for the expression and maintenance of complex dyadic relationships. The lemur data also highlight that between seasons (with the same group size) it is the social dynamics and relationships within the troop that influence the frequency of social monitoring.

Sussman et al. (2005) presented an elegant case for the importance of cooperation and affiliation over less frequently occurring agonism and competition in shaping in primate sociality. Accordingly, if agonism is infrequent, why would social monitoring be shaped by this sporadic behaviour? Primate socio-ecological models (Isbell & Young, 2002; Sterck, et al., 1997; van Schaik, 1989) have emphasised the role of competition in the evolution of primate sociality. Studies of social monitoring have followed this trend, despite data that indicate how friendly and cooperative interactions characterise primate interactions (Sussman et al., 2005) and social integration enhances reproductive fitness (Silk et al., 2003).

In free-ranging primates, the role of agonistic and competitive influences on social monitoring is less defined than that observed in the captive studies. Although agonism is important, the frequency of social monitoring cannot solely be attributed to the simple statement: higher aggression equals higher social monitoring. In sum, both studies 1 and 2 emphasised a complexity of social monitoring which has rarely been considered. It is difficult to speculate about the functions served by social monitoring, given that roughly 12% of visual time (across all contexts) was allocated to social monitoring. However, the findings suggest that social

monitoring is flexible and is used in accordance to context, changes in social dynamics (Jack, 2001; Keverne at al., 1978; chapter 3), and within-group social relationships that clearly differ among species (chapter 5). Although in this study group size accounted for a significant proportion of variance in social monitoring, additional social variables were important. The influence of affiliation on social monitoring lends support to arguments that agonism may not be the only driving factor in primate sociality (Sussman et al., 2005). Applying these principles from primate social behaviour to social attention, would also emphasise that social attention is not necessarily associated with agonistic and competitive influences. Further studies of vigilance with more groups and a wider range of species are needed to confirm this. The balance of social vs. non-social monitoring may be particularly important to consider. Despite the presence of predators (e.g. leopards) for the study group of baboons, more monitoring of social targets than non-social targets occurred. This suggests that social monitoring may also play a role in being vigilant against predators (Treves, 2000).

This chapter takes a first step towards assessing the interactive nature of social monitoring in primates. Many questions remain unanswered but as a starting point, it is clear that the frequencies of social monitoring vary according to a number of factors. The studies also provide support for the idea that competition and agonism are not the only driving factors concerning social monitoring in primate groups.

CHAPTER 8

PLACING SOCIAL MONITORING IN PERSPECTIVE

Overview

There are many important issues pertaining to primate visual attention, particularly concerning why primates visually monitor conspecifics in the group. In this thesis, I addressed some of these issues beginning with placing social monitoring within an overall perspective on primate vigilance. This considered issues including: a) how social monitoring fits into an overall visual attention budget, e.g. if social monitoring is not occurring, what is an individual doing with their visual time instead; b) the effect of context on visual attention, e.g. why social monitoring does not occur equally in all behavioural contexts.

Social monitoring was also considered using a social approach: applying principles from primate social behaviour to interpret social attention. A major advance was made on previous studies of social monitoring by conducting analyses of social monitoring within dyads and investigating the influence of social behaviour patterns such as affiliation, rank and agonism to evaluate why conspecifics within the social group are not monitored equally or monitored at all. In turn, I evaluated Chance and colleague's (Chance, 1967; Chance & Jolly, 1970) attention structure theory in primates with weak rank relationships and within free-ranging species to determine if dominance or agonism was the common basis for social monitoring.

A fourth and brief approach identified a complementary aspect of social monitoring: how monitoring conspecifics was used to determine how to

react to a novel or ambiguous event. Finally, I used a comparative approach to visual attention to determine how social monitoring was linked to social structure and within-group social relationships. Importantly, the focus concerned how social monitoring relates to the quality of social relationships within the group.

Based on the studies detailed in this thesis, I conclude that social monitoring is much more complex than previously thought. Visual attention is multi-faceted, responsive to and dependent on context, seasonal factors and social and environment events occurring at the time. Consequently, whether the underlying basis for social monitoring is stable over time or varies with group composition remains unknown. Only further long-term intra- and inter-specific studies can answer this question.

I have identified seven important issues for the study of social monitoring that are discussed further in this chapter. In the first part of this chapter I explore: a) why relationship quality is so important to understanding patterns of social monitoring; b) how, or indeed if, rank order is important for studying social attention; and c) why species differences exist in social monitoring.

In the second part of this final chapter, discussion concerns: a) time budget issues such as the amount of visual time spent monitoring conspecifics; b) the evaluation of using a 'social' approach to social monitoring; c) a consideration of the role that context plays in visual attention; and finally, d) how social monitoring and non-social monitoring might become intertwined in some 'cognitive' manner with the use of conspecifics as behavioural referents or informants about environmental

events. This chapter concludes with a critical evaluation of what is (now) known about social monitoring and the questions remaining to be answered.

Why relationship quality shapes patterns of social monitoring

In this thesis, relationship quality was one of the most important variables influencing social monitoring in all species. Relationships vary in quality and the prominence of affinitive or agonistic relationships vary within and between species. The relative importance of both positive aspects of social relationships, e.g. affiliation, and negative aspects, e.g. agonism, have been considered in detail. In this section, I explore why relationship quality shapes social monitoring.

Affiliation and monitoring friends

Social monitoring was found to have an affiliative basis, in most classes and species with the exception of orang-utans. That is, social monitoring occurred more frequently in friendly dyads than non-friendly dyads, and there were strongly positive correlations between social monitoring and affiliative relationships. Two additional indicators of good relationship quality - proximity and reciprocity (Silk, 2002) - were also applicable for interpreting patterns of social monitoring.

The benefits of keeping track of friends may outweigh those of monitoring adversaries. Sussman et al. (2005) argue for the importance of cooperation and affiliation in the evolution of primate sociality. Their evidence indicates that affiliative interactions represent the overwhelming majority of primate social interactions and highlights the need to understand how

individuals are able to maintain affiliative and coordinated behaviours within their social groups. Similarly, the ability to operate effectively in a social group is likely to depend on the ability to manipulate and anticipate the behaviour of conspecifics (Dunbar, 1988) in which social monitoring may play a role.

Although the benefits of friendships are likely to vary between species, for all social primates an important use of visual attention would be keeping track of friends (Dunbar, 1988). Given that primate agonism occurs much less frequently than prosocial behaviours (Sussman et al., 2005) and visual attention is costly in term of time and energy (Treves, 2000), attention should be directed towards friends and frequent interactants. This may function to regulate proximity with preferred partners (Rowell & Olson, 1983), initiate affiliative interactions (Strayer & Gariepy, 1986), and maintain visual contact with allies (Dunbar, 1983). Additionally, affiliates may participate in inter-troop encounters together (Mitani et al., 2002b; Nakamichi & Koyama, 1997) and form alliances (de Waal, 1982; Watts, 2002), behaviours that suggest visual monitoring of supportive individuals. Accordingly, visual tracking of friends and allies may play a more important role than the tracking of adversaries.

Proximity is not the cause of monitoring affiliates

Lemur data on the proximity of the target of social monitoring support an affiliative basis of monitoring. Friends were often monitored in proximity and importantly, non-friends were as likely as friends to be in proximity. The following question could be raised: were lemurs simply monitoring their

nearest neighbours? The data suggest not; lemurs did not simply look at those that were closest. Friends were monitored more than non-friends across all proximity categories, suggesting friends are selected as targets of attention.

An additional measure of cohesiveness was applied to all species (chapter 7) to determine if individuals that were more solitary or peripheral monitored conspecifics less frequently than individuals that often had nearest neighbours. Cohesiveness did not account for a significant proportion of the variance in social monitoring. This is important for interpreting effects of group size and captivity on social monitoring. A captive group could have more close associates within view due to less space, while a larger and free-ranging group could be more dispersed over a large area, resulting in less cohesiveness, but this was not the case in this study.

Reciprocal attention is a characteristic of friendly dyads

Strong social relationships are characterised by complementary contributions of both dyad members in affiliative interactions (Hohmann et al., 1999; Manson et al., 1999; Silk et al., 1999; 2006b; Watts, 2002). Traditional approaches to social monitoring have emphasised the inequality of attention, especially when considering rank influences on social monitoring. In chapter 4, weak social relationships in baboons were characterised by one dyad partner being primarily responsible for most attention exchanged within dyads. Reciprocity of attention within dyads therefore reflects the strength of the relationship; firstly, by the amount of visual time allocated to the partner, and secondly, by attention received from the partner. This suggests that

keeping track of some friends may be a mutual behaviour, at least visually, with both partners contributing equally to attention within the dyad.

Monitoring adversaries

The function of social monitoring has typically been associated with monitoring the level of threat or competition within a group. Primates may face severe levels of conspecific threat and thus are concerned with the actions of associates because these can have serious fitness consequences (Treves, 1998b; 2000). More frequent social monitoring occurs in individuals that receive high rates of agonism (Keverne et al., 1978; Pannozzo et al., 2007) and in some subordinate individuals (Caine & Marra, 1988; Emory & Harris, 1981a; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998; Pannozzo et al., 2007). The problem with these approaches is that the target of monitoring is not always clarified; e.g. does the recipient of aggression monitor their aggressor? While monitoring adversaries is important, evidence exists that affiliates in addition to adversaries are monitored frequently (Emory, 1976b; Virgo & Waterhouse, 1969; Waterhouse & Waterhouse, 1976; Watts, 1998).

Social monitoring in orang-utans and male lemurs (mating season) reflected agonism. The influence of both agonism and affiliation was also important for baboons and siamangs. Weak social relationships may facilitate monitoring of adversaries, especially if the relationship is unpredictable (Watts, 1998). However, social monitoring in baboon and male lemurs was not exclusively agonistic because attention was also directed towards female friends. This emphasises the benefit of considering attributes

of the target of monitoring, and multiple behavioural correlates of social monitoring, as the influence varies as a function of the composition of dyads in which individuals interact. Accordingly, social monitoring reflects: a) the status of relationships; b) the level of tension within the group; and c) an individual's own proclivities (Dunbar, 1988). Most primate social interactions are affiliative (Sussman et al., 2005) but if agonistic interactions outweigh affiliative interactions, social monitoring reflects this behaviour bias.

The interplay between affiliation and agonism on monitoring

Close relationships, evidenced by grooming and/or proximity, are sometimes negatively associated with agonism (Silk, 2002). However, friendships or close bonds do not necessarily confer a reduction in agonism in a number of species (Bernstein, 1991; Chivers, 1974; Fischer & Geissmann, 1990; Gould, 1996b; Smuts, 1985). This may be because rates of agonism can vary as a function of time spent in proximity (Smuts, 1985) and kinship (Bernstein, 1991). These findings are difficult to reconcile in terms of assessing the basis of social monitoring, but suggest agonism and affiliation are not always independent facets of behaviour, at least for influencing social monitoring. Social monitoring in baboons and siamangs was influenced by both affiliative and agonistic relationships, so it may be the case that monitoring reflects both nervousness and the desire to remain close to a conspecific (Dunbar, 1988). However, the baboon data suggest that social monitoring was directed towards both affiliates and adversaries.

It is important to note that agonistic interactions in the study species were relatively low intensity and rarely involved contact aggression. This may

explain why affiliation particularly influenced social monitoring, especially if the level of conspecific threat was relatively mild. Future studies assessing the level of conspecific threat in shaping patterns of monitoring would benefit from assessing the level of conspecific threat in terms of the risk of serious injury. Importantly, even when adversaries are monitored, visual time is still expended on monitoring affiliates.

Social monitoring is responsive to changes in competition

Social monitoring is usually considered as responsive to conspecific competition within the group. I considered feeding context as a time of heightened competition. However, social monitoring occurred at a lower rate in this context compared to resting. Glances to conspecifics were more indicative of attentional demands rather than feeding competition.

Instead, the changes in competition may facilitate social monitoring. Specifically, if social relationships change, and competition increases (e.g. during mating season), then social monitoring mirrors this social instability (Keverne et al., 1978; Treves, 1999; chapter 3). During the lemur mating season, it may be the case that increased rates of social monitoring are accounted for by increased attention to both rivals and potential mating partners, and data from chapter 3 suggest this. While Treves and Baguma (2002) and Caine and Marra (1988) suggest that competition accounts for species differences in social monitoring, only data on social relationships within the species can confirm this (chapter 5).

Implications of considering relationship quality on social monitoring

Throughout this thesis, emphasis has been placed on categorising social relationships and thus interpreting social monitoring based on relationship quality. From the outset, social monitoring was considered as a dyadic interaction involving two individuals. Specifically, information on the attention structure of primates could not be meaningfully gained by considering simply how often an individual monitors without considering the targets of monitoring. This is why Chance and colleague's theory (Chance, 1967; Chance & Jolly, 1970) did not address attention structure within a wider social context and perhaps why subsequent studies on social attention have not unequivocally found support for the theory (Dunbar, 1983; Haude et al., 1976; Strayer & Gariepy, 1986; Torres de Assumpção & Deag, 1979). The use of relationship quality as an index of social monitoring permits comparative assessment of social monitoring in multiple species (whether a rank hierarchy is present or not) and attempts to address why certain dyads monitor more frequently than other dyads.

While the use of relationship quality in interpreting social monitoring patterns was useful, more information would be gained if dyads were classed using affiliation and agonism considered together rather than separately e.g. a friendly dyad with low agonism, or a friendly dyad with high agonism. This would help ascertain whether ambiguity in the social relationship results in differential patterns of social monitoring. Additionally, dyads classed as non-friends were not necessarily agonistic. Many dyads were characterised as neutral, exhibiting low aggression and low affiliation and this was often the

case for orang-utans. Therefore, when considering relationship quality, a larger sample size would permit dyads to be classed more thoroughly.

Are rank relationships important for social monitoring?

This thesis provides evidence that important social behaviours other than rank relationships account for social monitoring in primate populations. Past studies did not consider alternative mechanisms of social monitoring, and have not evaluated whether rank provides the most accurate representation of attention structure in primates.

When species with clear rank hierarchies were considered, it was clear that rank status (of individuals and within dyads) did not influence social monitoring in lemurs and chimpanzees. The only effect of rank on monitoring was in the opposite way predicted by the attention structure theory. In baboon female-female dyads, dyads closer in rank tended to monitor more frequently than those more distant in rank. Two other points merit further mention. Male lemurs during birth season (subordinate to all females) monitored less frequently than the females. Baboon females (subordinate to all males) monitored some males as equally as the male monitored her. These findings suggest that rank influences on social monitoring are not as influential as previously considered, and results from chapter 7 confirmed that rank was not a significant predictor of social monitoring in the study species.

This is the first study to examine rank based social attention in free-ranging primates, and for these study species at least, rank order did not

influence patterns of monitoring in the way the attention structure theory would have predicted.

Species differences in social monitoring

In terms of the frequency of social monitoring, species differences may simply reflect an effect of natural group size, in terms of the number of associates available to monitor. However, group size is not unambiguously associated with social monitoring. The siamangs monitored at higher frequencies than the other apes even though group sizes were comparable. Primate social organisation is incredibly diverse, so the basis of social monitoring varies between species as a function of the social relationships within the groups. Few comparative studies of social monitoring exist, and they provide conflicting results. However, it is important to attempt to unravel species differences in social monitoring, and I have made progress in part by using consistent methodology in the study groups.

The size of primate groups

Although group size within the same species does not influence vigilance (e.g. Treves, 2000) or social monitoring (Treves, 1999), group size seems important when taking a comparative approach to social monitoring (Treves, 1999) simply because primate species vary considerably in group size. This is problematic for a number of reasons. There is an assumption that if there is a group size effect on social monitoring, then all individuals are monitored equally. This means that social monitoring would invariably be higher in larger groups as both a function of competition and more targets to monitor.

The initial chapters provided substantial evidence that individuals are not monitored equally. The results of chapter 7, however, indicated that group size was an important predictor of the frequency of social monitoring. Does the large amount of variance accounted for by the regression model of social monitoring reflect species differences, or an absolute function of group size? This question could not be answered fully as for most species only one group was studied. Within orang-utans, however, multiple groups were studied and the largest group of four monitored conspecifics at a lower rate compared to orang-utans housed in pairs, or trios.

Treves (1999) reported higher rates of social monitoring in colobus monkeys compared to redtail monkeys, consistent with the larger size of the former group. Smaller groups of howler monkeys monitored conspecifics less frequently than the other species (Treves & Baguma, 2002). In chapter 7 (like in Treves 1999), group size accounted for considerable variance in the frequency of social monitoring in all the species considered together. Once group size was controlled, other social variables also accounted for sizeable variance in social monitoring.

It seems paramount to ensure that study groups are of representative size given the species. The biggest concern for my study was that the captive chimpanzee study group was considerably smaller than the reported range of 20-150 individuals in wild chimpanzee communities (Newton-Fisher, 1999; Nishida & Hiraiwa-Hasegawa, 1987; Stumpf, 2007; Watts 2002). Although chimpanzees fission to form small parties (consisting of usually less than six members), these parties frequently change in size and composition

(Nishida & Hiraiwa-Hasegawa, 1987). It is likely that important characteristics of chimpanzee sociality are difficult to capture in small, captive populations.

Social organisation

Social organisation has been emphasised as a critical influence on the propensity to monitor conspecifics (Chance, 1967; Chance & Jolly, 1970). The problem with considering social monitoring as a function of social organisation is that species on the whole are categorised based on the level of presumed competition. This approach is supported by the influence of social organisation on social monitoring particularly during feeding context. Despotic species are reported to monitor more often during feeding than egalitarian species (Caine & Marra, 1988; Treves & Baguma, 2002). This issue was addressed in chapter 7 by considering social monitoring in different contexts as a function of species. The use of glances compared to looks was also analysed, partly to evaluate the influence of context on visual attention, but also because competition may be associated with the use of social glances (Blois-Heulin & Girona, 1999).

In chapter 7, there was some evidence for the influence of social organisation on monitoring conspecifics. Orang-utans, a semi-solitary species, engaged in less social monitoring than the other species; and baboons (a multi-male species) engaged in more social monitoring than the other species. While the data from this chapter indicated that baboons glanced more frequently at conspecifics than did the other species, they glanced in both resting and feeding contexts. This could be interpreted in one of two ways: baboons experience competition in all contexts hence the use

of social glances, or because individuals in large, dynamic groups have additional demands on their attention in the form of more conspecifics to attend to, and the presence of predators, in addition to demands such as procuring and processing food. The latter explanation is supported by the fact that baboons also used both social and non-social glances significantly more often during feeding compared to resting.

Why social monitoring may differ among species

Social influences on social monitoring vary according to within-group relationships. Classifying species, for example, as monogamous and co-operative, informs little about how the relationships are maintained and how visual attention may feature in the relationship. Similarly, classification of groups as multi-male implies male competition may be higher, yet in mating seasons, thought to be a time of intense male competition, males in both uni-male and multi-male groups increase their social monitoring (Treves, 1999). Data from chapter 5 indicate that similar rates of social monitoring in siamangs and chimpanzees were the result of the social bonds within the group, especially as chimpanzees and siamangs have very different social structures. The orang-utan data also highlight variability in social monitoring as a function of different social relationships within separate groups. If this is the case, then the motivation to monitor conspecifics may vary in different social groups, even within the same species. Accordingly, social monitoring may be related to group dynamics rather than species differences. Clearly, background information on basic social behaviour in multiple groups would

provide a clear quantitative measure of group dynamics as a function of species.

How important is social monitoring for primates?

Visual attention budget

Primates spend a considerable amount of time monitoring conspecifics (Treves, 2000) yet little is known about how social monitoring fits into an overall visual attention budget. Within a visual attention budget framework, I examined the percent of visual time allocated to monitoring conspecifics. Difficulties in comparing visual budgets of primates are usually related to inconsistent methodology between studies; therefore, frequencies of social monitoring are problematic to compare.

The percentage of time spent monitoring conspecifics varies from approximately 3% in wild capuchin monkeys (Jack, 2001) to as much as 59% in some captive species (Torres de Assumpção & Deag, 1979). In my study, the percent of social monitoring ranged from 4% (orang-utans) to 17% (baboons). This seems like a relatively low figure, in comparison to some captive species, and no studies of social monitoring can provide a comparison for the species that I studied. However, vigilance data for wild primates could determine if comparable results are evident for each species studied.

If all vigilance is considered, the study species spent roughly 30% of their visual budget being vigilant (ranging from 22% in the orang-utans to 36% in lemurs and siamangs). Kutsukake (2006) reported that free-ranging chimpanzees spent roughly 40% of time engaged in vigilance whilst resting.

Free-ranging gibbons spend approximately 50% of observed time vigilant (Uhde & Sommer, 2002) and baboons are vigilant 30-60% of observed time (Hill & Cowlishaw, 2002). Vigilance estimates for wild orang-utans (Setiawan et al., 1997) and birth season ring-tailed lemurs (Gould et al., 1997) are lower (2% and 7-10% observed time respectively) than vigilance estimates in my study. However, orang-utan social encounters are rare in the wild (McKinnon, 1972; 1974) and Gould et al. (1997) reports a vigilance estimate that excluded monitoring of intra-group conspecifics.

What is clear from past studies is that captive environments appear to promote a higher incidence of social monitoring. In this thesis, both captive and free-ranging primates were considered, and all species spent less than 20% of visual time monitoring conspecifics. Based on the figures, the data from the captive groups are comparable to vigilance estimates reported in wild populations (probably due to enriching naturalistic environments and appropriate group composition).

Using a 'social' approach to social monitoring

Chance's contribution

In this thesis, I have emphasised the importance of relationship quality in assessing social monitoring using measures of affiliative, agonistic and rank behaviours. The importance of relationship quality became apparent when studying Chance and colleague's attention structure theory. This theory received some early support but much of this support did not involve hypothesis testing nor quantitative data analysis on the structure of attention in primates, just more theorising. Furthermore, visual attention was not

necessarily measured in some studies. Allogrooming has been used as a proxy for social attention (Reynolds & Luscombe, 1976; 1969), and the definition of attention may not be explicit enough to permit replication (Virgo & Waterhouse, 1969; Waterhouse & Waterhouse, 1976).

Subsequent studies have generally focused on the premise that: a) subordinates monitor more frequently than dominant animals; b) dominant animals receive more attention than subordinates; and c) the higher the rates of aggression received, the higher the rates of social monitoring. There is some support for social monitoring as a means of protecting against threat (Emory & Harris, 1981a; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998; Pannozzo et al., 2007; Pitcairn, 1976). However, frequent attention is also directed to salient targets such as play partners (Emory, 1976b), allies (Dunbar, 1983) and grooming partners (Virgo & Waterhouse, 1969; Waterhouse & Waterhouse 1976). Accordingly, agonistic and competitive interactions (Strayer & Gariepy, 1986) and rank relationships (Dunbar 1983; Torres de Assumpção & Deag, 1979) do not characterise the basis of social monitoring in all primate groups.

Keverne et al. (1978) have argued that although the alpha animal receives the most attention, they are not necessarily the most aggressive. This is why relationship quality is important; classifying an individual as high-ranking based on winning agonistic encounters, informs little else about the proclivities of the individual apart from the ability to acquire resources.

Rank based attention in middle-ranking individuals is also puzzling and rarely addressed. As middle-rankers are both potential recipients and initiators of aggression, they may directly monitor all conspecifics equally

(Emory & Harris, 1981a) or monitor more frequently than both dominant and subordinate individuals (Haude et al., 1976). Another discrepancy concerns the inclusion of infant or juvenile animals in the study group; usually classed as subordinate. Young primates may use social monitoring with very different motivations, for example as a form of learning about the environment rather than a function of low status (Kaplan & Rogers, 2000; Querouil & Blois-Heulin, 1997; chapter 6).

The presence of a rank based attention structure has only been identified in captive populations. Additionally, rank is used as an attribute of an individual rather than of a dyadic relationship. This is problematic and raises questions whether rank based attention structures exist in free-ranging species. My studies, albeit on a limited number of species, support the idea that other social behaviours are more important for explaining the basis for social monitoring even in groups possessing hierarchical dominance (chapter 7).

The importance of dyadic relationship quality

Social monitoring cannot be considered a quality of an individual because social monitoring is a characteristic of social partners in a relationship. Without knowing who an individual is looking at, it would be unjustified to conclude that low status equates to increased social monitoring. Most analytical approaches to social monitoring involve summing targets of monitoring (across all individuals) to examine rank effects. It is possible that monitoring of both adversarial and affiliative targets facilitates high rates of social monitoring when there are a greater number of important targets within

the group to keep track of. In this thesis, analysis of dyads provided an appropriate approach to understanding the patterning of social monitoring. Social behaviours are usually assessed using dyads (e.g. Hemelrijk, 1990) and dyads are relevant for social monitoring given that social monitoring is an interaction involving two individuals. Like social behaviour, the contribution of attention differs between dyad partners.

Applying principles of social behaviour to visual attention identified several similarities in visual behaviour compared to social behaviour, namely that social monitoring reflects the strength of the social bond (chapters 3-5) and in strong relationships, both partners contribute to maintaining visual attention in the dyad (chapter 4). Reciprocity in visual behaviour from both dyad partners reflects the strength of the relationship, as evident for affiliative interactions such as grooming (Hohmann et al., 1999; Manson et al., 1999; Silk et al., 1999; 2006b; Smuts, 1985; Watts, 2002).

A major drawback of assessing social monitoring in dyads concerns the limited data analytical tools available for non-independent dyadic data. This may explain why the individual is frequently the unit of analysis (Kenny et al., 2006). However, the benefits gained from assessing dyads in terms of relationship quality, the symmetry of monitoring, and frequency of monitoring within and between dyad partners outweigh the difficulties associated with assessing dyadic data. By not considering relationship quality for each dyad within the group, and not assessing the targets of monitoring, current knowledge on social monitoring is incomplete. Further studies using a social approach would gain a more complete picture of social influences on visual attention.

The influence of context on social monitoring

Context was considered in detail to answer several questions. It is well documented that context influences vigilance. However, to gain a complete picture, data on social monitoring were collected throughout the day, reflecting the activities that the primates engaged in. In chapter 7, social monitoring during feeding was compared to the resting context to address whether context influences social monitoring in the same way it influences overall vigilance, whether feeding competition heightens social monitoring and whether context necessitates the use of glances.

Vigilance in feeding compared to resting context

Attentionally demanding activities reduce vigilance (Chalmeau et al., 1998; Hill & Cowlishaw, 2002; Hirsch, 2002; Kutsukake, 2006; Maestripieri, 1993a; van Schaik & van Noordwijk, 1989; Treves, 2000; Treves et al., 2001; Uhde & Sommer, 2002). However, the amount of visual attention portioned to social targets is thought to be facilitated rather than compromised during feeding as a result of competition (Blois-Heulin & Girona, 1999; Blois-Heulin & Martinez-Cruz, 2005; Treves & Baguma, 2002).

In chapter 7, social looks rather than glances were reduced during feeding, supporting an overall decrease in vigilance as previously reported. Furthermore, the use of both social and non-social glances appeared to offset some of the visual costs of feeding, particularly by the larger groups in order to balance vigilance regarding the environment, conspecifics and eating.

A multi-faceted model for social monitoring across contexts

Taking a multi-variable approach to social monitoring is important for identifying influential variables. For instance, interactions between variables such as attention types and targets, or, context and species, depend on the levels of the other variables. Additionally, if group size accounts for all the variance in the frequency of social monitoring, it may be pointless to compare species that naturally differ in their group size from other primates. While group size in chapter 7 accounted for a significant proportion of variance, other social variables also accounted for significant variance in rates of social monitoring.

Affiliation accounted for a considerable amount of variance in feeding context social monitoring. Keeping track of friends may be important for obtaining access to resources or promoting co-tolerance during feeding (Koyama, 2000). In contrast, across all contexts and during resting, received aggression played a role in influenced social monitoring, but this effect was moderated by group size. My study found that frequently received aggression reduced social monitoring in large groups but facilitated social monitoring in small groups, and this is of primary importance for interpreting the role of threat protection in social monitoring. These findings may therefore account for agonistic influences of social monitoring obtained in previous studies involving small, captive groups of primates.

Additionally, analysis of social monitoring in other contexts would provide even greater information on contextual influences on visual attention. For instance, self-directed behaviour is an indicator of anxiety (Maestripieri, 1993b; Troisi & Schino, 1987), therefore consideration of social monitoring

during this behaviour would help address if social monitoring is an index of nervousness (Dunbar, 1988). A final issue concerns the frequency of social behaviours during different contexts. Documentation of the contexts in which affiliation and agonism occurs would help strengthen the case for contextual and social influences on social monitoring. For instance, clumped food compared to dispersed food results in higher rates of social monitoring, and higher rates of positive as well as negative social interactions (Blois-Heulin & Martinez-Cruz, 2005).

Using visual attention to reference conspecifics

The social referencing study has implications both for considering why conspecifics may be looked at, and cognitive-developmental processes of social referencing. Although social referencing occurred rarely in response to naturally occurring events, social referencing in all orang-utans could be induced at least once by the use of long call playbacks: an unfamiliar and potentially alarming stimulus.

Social referencing is a powerful learning process that accounts for learning in human children (Feinman et al., 1992). However, due to the high adaptive value of social referencing (e.g. for assessing threats, detecting predators, and determining palatability of food) social referencing may continue through adulthood. Like human infants, young primates may lack the experience in order to react appropriately, therefore the alternation of gaze between a stimulus and a referent is considered an active solicitation for information (Russell et al., 1997) either to learn about a stimulus or seek protection from a stimulus. However, adults may also reference other adults

when stimuli are biologically relevant and/or ambiguous (chapter 6). The greater number of referential looks elicited by an unfamiliar long call in the youngest orang-utans suggested they were actively seeking information. It may be the case that referencing conspecifics in younger individuals concerns a request for information on how to react, while in adults, more specific information may be required such as 'what was that'?

Why social referencing is more than looking at conspecifics

Social monitoring throughout this thesis has been defined as visual attention to conspecifics. Social referencing by definition requires the modulation of attention between an object/event and a conspecific (referential attention). What is interesting though is that social monitoring, i.e. non-referential looks, increases after presentation of a novel object (Roberts et al., 2008) or vocalisation (chapter 6). While alternating attention is considered an active request for more information (Russell et al., 1997), increased social monitoring after an event or presentation of an object may still provide information.

Baldwin & Moses (1996) suggest that observational learning from conspecifics (Cook et al., 1985; Mineka et al., 1984) differs from social information gathering, as observational learning does not require comprehension of another individual as a source of information. Additionally, an individual might profit from a conspecific's behaviour without having actively referenced them, and without recognition that information has been gained (Baldwin & Moses, 1984). Using this perspective, while social monitoring may be useful for gathering social information, social monitoring

on its own is not an active request for information from other more knowledgeable conspecifics. It is unclear whether only great apes possess the cognitive mechanisms needed to recognise, solicit and use visual social information (Russell et al., 1997; chapter 6). Clearly, in primates, the role of social visual attention in information gathering processes needs to be identified in more detail.

What is known about social monitoring that was not known before

One of the most important findings in this thesis is that social monitoring is indicative of the strength of social relationships, both in terms of affiliative and agonistic relationships. The studies documented in this thesis also refute the interpretation of rank ordered social attention structure. It is possible that rank ordered social monitoring could be an artifact of captivity, but this is difficult to confirm because no studies of free-ranging primates have examined rank influences on social monitoring.

The main benefit of this thesis, to primate social research, concerns the comparative analysis of social monitoring in five understudied species of primates (in terms of visual attention research), compared on variables such as social bonds, agonism, rank, context and attention type using a consistent and detailed methodology. Additionally, the studies on the baboons and lemurs provide a first look at attention structure in two free-ranging primates, an area where research is clearly lacking. This research contributes to wider knowledge on social monitoring but more specifically, the nature of social monitoring within a dyad and the influence of the social relationship on the exchange of visual attention between two individuals. This perspective allows

principles of primate social behaviour to be applied to data on social monitoring to specify the roles played by all variables of interest in characterising social behaviour.

The findings indicate that social monitoring is complex. No single variable can account for social monitoring relevant for different contexts and for each species. This is important given that the species studied did not differ much in the time spent vigilant. Species differences were more evident, however, when considering how attention was apportioned to social and non-social targets. Consideration of non-social monitoring is useful in determining, for instance, if only social monitoring increases during feeding or whether attention types such as the use of glances are restricted to conspecifics. While social factors influence visual attention, visual attention in general is also influenced by context. Accordingly, the underlying basis of social monitoring may vary according to context, motivation and function and these are important aspects that studies need to take into account. If the basis for social monitoring is different during feeding (e.g. affiliative individuals monitor more frequently, chapter 7) then species that spend considerable time feeding, e.g. folivorous primates, may have a different attention structure compared to primates that spend less time feeding.

The stability of the underlying basis of social monitoring appears to be different for males and females, and differs from the birth to mating season (at least in lemurs). Social monitoring in male lemurs is responsive to seasonal changes in within-troop dynamics, with monitoring adjusted to reflect increasing levels of male-male competition and to find a mate. It is also the case that some environmental events influence social monitoring.

For orang-utans at least, monitoring conspecifics occurs more frequently following a salient event. It remains unknown whether this type of monitoring is different from spontaneous monitoring. However, the alternating of attention following an event would suggest that an event that elicits monitoring may be different in terms of the motivation to look at conspecifics.

What still remains unknown about social monitoring

Although social monitoring occurs at a greater frequency towards friends, the benefits served by monitoring friends are speculative. Knowledge of kin relationships would be useful in determining whether unrelated individuals or family members are monitored more frequently. This would help when examining social monitoring in monogamous primates. The data on lemurs indicated some strong effects of proximity on social monitoring. However, less global proximity categories would determine whether monitoring simply occurs to those individuals closest spatially. The proximity of neighbours when individuals are not monitoring would help determine: a) if monitoring is influenced by the number of neighbours present, as more neighbours equal more individuals to monitor; b) whether individuals more proximate to an individual are monitored less frequently - peripheral vision may negate monitoring very close conspecifics; and c) whether friends compared to non-friends situated the same distance away from the focal are monitored unequally.

The evaluation of why primates monitor conspecifics would be strengthened if visual monitoring was demonstrated to benefit an individual in some way. For instance, perhaps individuals that are more vigilant are better

able to avoid aggression compared to less vigilant individuals. Alternatively, perhaps individuals that engage in frequent and reciprocal social monitoring are more likely to support one another in conflicts, or in defence of territory.

Long-term studies of social monitoring are needed to determine how social monitoring may be altered in periods of social change such as mating season, or rank hierarchy changes. Month by month patterns of both social monitoring and social behaviour would help address the influence of social behaviour changes on visual attention. Accordingly, higher rates of social monitoring may occur as a function of natural group size, e.g. more individuals to monitor, or simply that more attention-capturing events occur in particular groups. Data on why individuals are monitored, e.g. an individual vocalised or is approaching, would help differentiate between spontaneous looks compared to attention elicited by a conspecific event. Data on behaviour following social monitoring would also be revealing. For instance, if a friend is monitored, is proximity sought or an affiliative interaction initiated?

Given that context, agonism and affiliation are influential on social monitoring, breaking down social behaviour occurrences during different contexts would help explain predictors of monitoring that vary between contexts. For instance if agonism occurs most frequently during feeding, and affiliation during resting, the motivation to monitor conspecifics may function in accordance with the behavioural context, indeed the data in chapter 7 suggest this.

Many of these unanswered questions could be addressed if multiple groups of the same species were studied. This would examine whether

larger groups monitor more frequently, whether social relationships within troop members of the same species differ, and whether periods of instability affected groups in the same way. Currently, it is difficult to identify if the differences in social monitoring between species reflect group size, differences in group social dynamics or real species variation in social monitoring.

This thesis has focused on intra-group social monitoring; however, inter-group monitoring is another important component of social visual behaviour. The orang-utan data suggest a significant component of visual time is directed towards conspecifics outside the social group. The division of vigilance into anti-predatory vigilance, and social monitoring occurring outside and within the social group would be more informative. For instance, if the level of external threat is high (whether from predators or extra-group competitors) then attention may be diverted outside the group rather than within. This area clearly merits further study.

Research limitations

As could be expected in a thesis, research periods were relatively short (three months maximum). The short periods of study time meant that the data captured what was occurring in the group at the time; thus longer term studies would be imperative for evaluating the stability of social monitoring. While the lemur data indicate that social monitoring is responsive to seasonal changes in behaviour, further research is needed to confirm whether social monitoring returns to pre-mating season levels. In free-ranging primates, social groups rarely remain stable: individuals are born, emigrate, immigrate

and are eaten by predators. Consequently, seasonal variations in social monitoring are important to consider.

Comparison of the same species studied in wild and captive settings could have been conducted to illustrate the influence of the captive environment on social monitoring. Alternatively, one could study multiple groups of the same species in the same setting to examine within-group variation. In this thesis, multiple groups of captive orang-utans were studied. This was helpful in illuminating the considerable variation in social monitoring based on group size and composition, but it is likely that social groups even of the same species differ considerably.

Coding visual attention behaviour is challenging. Attention changes frequently, so very frequent sampling is necessary. It is essential to record additional information whilst recording visual attention; thus, simultaneous recording of data in short time intervals is difficult. Some researchers are able to collect continuous data on vigilance and associated behavioural variables such as proximity, context, and height from ground, but this has been accomplished by sacrificing individual identification (Treves, 1998a; 1999; Treves et al., 2001) or by not specifying the targets of attention (Alberts, 1994; Altmann, 1980; Hirsch; 2002; Kutsukake, 2006; 2007; Rowell & Olson, 1983). Such data are inadequate for social monitoring. The use of point sampling allowed more than one type of data to be collected at once. Point samples allowed consideration of the target being monitored, the target's proximity, attention type and the behavioural context. Using 10-second point samples, I attempted to collect visual information as frequently as possible considering attention shifts occur rapidly. The main flaw of point

samples and particularly for attention research is that attention shifts may occur outside the 10-second signal. Using five-second point samples in free-ranging primates would have been extremely difficult and additional data on context or proximity would not have been collected. However, comparisons of the study species' vigilance to data collected in other studies demonstrated that there were not huge differences in estimates of vigilance, even though different methodologies were used. An alternative strategy would be to utilise video recordings of attention; however, this would not have been practical for free-ranging populations, especially if interindividual distance was great.

The duration of social monitoring could provide some useful insights into the effect of relationship quality on social monitoring; for instance if affiliative partners are monitored for longer durations. However, using continuous samples to measure duration of social monitoring might restrict this type of data collection to captive populations only.

Overall, studies on social monitoring, including this thesis, are likely to only have scratched the surface of primate visual attention. Social monitoring merits further investigation because it is frequent, may affect predator detection, could function in social learning and represent the strength of the social bond. This latter implication may be particularly important in assessing relationship quality in species where overt affiliative behaviours are rare.

Final thoughts

Does social monitoring reflect two motivational states: nervousness and keeping track of friends, as suggested by Dunbar (1988)? My research suggests keeping track of friends is an important motivation underlying patterns of social monitoring. Nervousness may well be the link between aggression received and social monitoring. The data in this thesis indicate that social monitoring depends on a number of factors. There is no single consistent variable that is applicable to all the study species and classes of dyads, but visual monitoring is likely to be a response to and adjusted in accordance with the social dynamics of the group. If relationships within a group are stable and friendly, then affiliation may be the most important indicator for social monitoring, as found in chimpanzees, birth season lemurs, and some baboons. If relationships within a group are ambivalent or neutral, then social monitoring may occur at a lower frequency and within dyads with a more agonistic relationship, as found in orang-utans. Finally, if there is frequent agonism within the group or unstable or ambiguous relationships, then attention may be directed towards agonistic partners, as evident in siamangs, baboon males and lemur males during the mating season.

In conclusion, social monitoring is a highly variable but important component of social behaviour. Understanding more about social monitoring may reveal how affiliative and coordinated behaviours are maintained within a group and provide insights into the evolution of sociality and group living in primates.

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